SHOUT
SHARE
IT

BRE
1508

HARVARD UNIVERSITY

Library of the
Museum of
Comparative Zoology

1508

BREVIORA

Museum of Comparative Zoology

HARVARD UNIVERSITY

NUMBERS 464–487

1981–1986

MCZ
LIBRARY

NOV 19 1986

HARVARD
UNIVERSITY

CAMBRIDGE, MASSACHUSETTS 02138 U.S.A.
1986

BREVIORA

MUSEUM OF COMPARATIVE ZOOLOGY

CONTENTS

NUMBERS 464–487

1981

No. 464. The Origin of the Crocodiloid Tarsi and the Interrelationships of Thecodontian Archosaurs. By Donald Brinkman. 23 pp. December 30.

No. 465. The Structure and Relationships of the Dromasaurs (Reptilia: Therapsida) By Donald Brinkman. 34 pp. December 30.

1982

No. 466. Systematics of the *Mexicana* Species Group of the Colubrid Genus *Lampropeltis,* with an Hypothesis Mimicry. By William R. Garstka. 35 pp. June 30.

No. 467. Three New Species of the *Anolis Punctatus* Complex from Amazonian and Inter-Andean Colombia, with Comments on the Eastern Members of the *Punctatus* Species Group. By Ernest E. Williams. 38 pp. June 30.

No. 468. A New Forest Skink from Ponape. By A. Ross Kiester. 10 pp. June 30.

No. 469. Catalog of the Primary Types of Bombyliidae (Diptera) in the Entomological Collections of the Museum of Comparative Zoology, with Designations of Lectotypes. By Neal L. Evenhuis. 23 pp. June 30.

No. 470. Systematic Implications of Innervation Patterns in Teleost Myotomes. By Quentin Bone and R. Dana Ono. 23 pp. June 30.

No. 471. Arthur Loveridge—A Life in Retrospect. By Ernest E. Williams. 12 pp. June 30.

No. 472. Fishes of the Suborder Labroidei (Pisces: Perciformes): Phylogeny, Ecology, and Evolutionary Significance. By Leslie S. Kaufman and Karel F. Liem. 19 pp. June 30.

1983

No. 473. The Interrelationships of Pelycosaurs. By Donald Brinkman and David E. Eberth. 35 pp. April 29.

No. 474. *Ruthiromia Elcobriensis,* A New Pelycosaur from El Cobre Canyon, New Mexico. By David A. Eberth and Donald Brinkman. 26 pp. April 29.

No. 475. New or Problematic *Anolis* from Colombia. I. *Anolis Calimae,* New Species, from the Cloud Forest of Western Colombia. By Stephen Ayala, Dennis Harris, and Ernest E. Williams. 11 pp. April 29.

No. 476. Townsend's Unmapped North Atlantic Right Whales *(Eubalaena Glacialis).* By William E. Schevill and Karen E. Moore. April 29.

1984

No. 477. New or Problematic *Anolis* from Colombia. II. *Anolis Propinquus,* Another New Species from the Cloud Forest of Western Colombia. By Ernest E. Williams. 7 pp. September 7.

No. 478. New or Problematic *Anolis* from Colombia. III. Two New Semiaquatic Anoles from Antioquia and Chocó, Colombia. By Ernest E. Williams. 22 pp. September 7.

No. 479. Agonistic and Courtship Displays of Male *Anolis Sagrei.* By Michelle P. Scott. 22 pp. September 7.

1985

No. 480. Three New Lizards of the Genus *Emoia* (Scincidae) from Southern New Guinea. By Walter C. Brown and Fred Parker. 12 pp. June 21.

No. 481. A New *Anolis* of the *Lionotus* Group from Northwestern Ecuador and Southwestern Colombia (Suaria: Iguanidae) By Kenneth Miyata. June 21.

No. 482. New or Problematic *Anolis* from Colombia. IV. *Anolis Antioquiae,* New Species of the *Anolis Eulaemus* Subgroup from Western Colombia. By Ernest E. Williams. 9 pp. June 21.

No. 483. Notes on *Pristidactylus* (Sqamata: Iguanidae). By Richard Etheridge and Ernest E. Williams. 18 pp. June 21.

No. 484. Male Aggressive Behavior in a Pair of Sympatric Sibling Species. By Jonathan B. Losos. 30 pp. June 21.

1986

No. 485. The Anatomy and Relationships of *Stereophallodon* and *Baldwinonus* (Reptilia, Pelycosauria). By Donald Brinkman and David A. Eberth. 36 pp. August 30.

No. 486. *Thelodus "Macintoshi"* Stetson 1928, The Largest Known Thelodont (Agnatha: Thelodonti). By Susan Turner. 20 pp. August 30.

No. 487. The Identity of Larval *Parasudis* (Teleostei, Chlorophthalmidae), with Notes on the Relationships of Aulipoform Fishes. By Karsten E. Hartel and Melanie L. J. Stiassny. 24 pp. August 30.

BREVIORA

Museum of Comparative Zoology

Index of Authors

Numbers 464–487

1981–1986

Ayala, Stephen 475

Bone, Quentin 470

Brinkman, Donald 464, 465, 473, 474, 485

Brown, Walter C. 480

Eberth, David E. 473, 474, 485

Etheridge, Richard 483

Evenhuis, Neal L. 469

Garstka, William R. 466

Hartel, Karsten E. 487

Harris, Dennis 475

Kaufman, Leslie S. 472

Losos, Jonathon B. 484

Liem, Karel F. 472

Miyata, Kenneth 481

Moore, Karen E. 476

Ono, R. Dana 470

Parker, Fred 480

Scott, Michele P. 479

Shevill, William E. 476

Stiassny, Melanie L. J. 487

Turner, Susan 486

Williams, Ernest E. 467, 471, 475, 477, 478, 482, 483

MUS. COMP. ZOOL.
LIBRARY
MAR 16 1982
HARVARD
UNIVERSITY

B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 30 DECEMBER 1981 NUMBER 464

THE ORIGIN OF THE CROCODILOID TARSI AND THE INTERRELATIONSHIPS OF THECODONTIAN ARCHOSAURS

DONALD BRINKMAN[1]

ABSTRACT. The tarsus of the proterosuchian *Chasmatosaurus* represents the primitive archosaur tarsus. This kind of tarsus is also present in rhynchosaurids, trilophosaurids, prolacertids, and *Protorosaurus,* and suggests that these reptiles are members of a single radiation. Two distinct kinds of crocodiloid tarsi are present in thecodonts, a crocodile-normal tarsus and a crocodile-reversed tarsus. The crocodile-reversed tarsus could have originated from the crocodile-normal tarsus, but the reverse relationship is not plausible. *Gracilisuchus,* the only "ornithosuchid" with a crocodile-normal tarsus, shows features of the skull that are not consistent with its placement in the Ornithosuchidae. *Euparkeria,* on the basis of both cranial and postcranial characters, is a plausible ornithosuchid ancestor but could not be ancestral to a pseudosuchian with a crocodile-normal tarsus. The tarsus of *Erythosuchus* neither contradicts nor supports a relationship between *Erythrosuchus* and rauisuchids.

INTRODUCTION

In recent years, it has been recognized that a number of structurally distinct kinds of tarsi are present in archosaurs, and an understanding of the evolution of this structural complex is necessary for an understanding of the interrelationships of the group. In the tarsus of crocodiles and typical pseudosuchians, the ankle joint passes between the astragalus and calcaneum, the astragalus being locked to the tibia and the calcaneum integrated with the pes. In dinosaurs, the ankle joint passes distal to the astragalus and calcaneum. Krebs (1963, 1973) argued that this

[1]Museum of Comparative Zoology, Harvard University, Cambridge, Massachsuetts 02138.

difference precludes derivation of dinosaurs from any known pseudosuchian. Recently, two additional kinds of tarsi have been recognized in thecodonts. Proterosuchian thecodonts of the family Proterosuchidae have a distinct tarsus that is in many ways primitive (Cruickshank, 1972; Carroll, 1976). Bonaparte (1971) recognized that two distinct kinds of crocodilelike tarsi are present in pseudosuchians, one like that of crocodiles in which the astragalus has a peg that fits in a socket on the calcaneum, and one seen in advanced ornithosuchids in which the calcaneum has a process that fits in a socket on the astragalus. Chatterjee (1978) termed these the crocodile-normal and crocodile-reversed tarsus respectively. Also, two pseudoschians with mesotarsal ankle joints have been described (Romer, 1971). One of these, *Lagerpeton,* has a fully developed mesotarsal joint. The second, *Lagosuchus,* retains a posteriorly directed calcaneal tuber and a complex articulation between the astragalus and calcaneum (Bonaparte, 1975a).

The evolution of these tarsal patterns was recently discussed by Cruickshank (1979). Cruickshank showed that the proterosuchian tarsus is an excellent structural ancestor to the crocodile-normal tarsus and argued that the two kinds of crocodile tarsi can be used to separate pseudosuchians into two groups. Based on this, Cruickshank suggested that *Gracilisuchus,* which has a crocodile-normal tarsus, be removed from the Ornithosuchidae, all other members of which have a crocodile-reversed tarsus. However, the origin of the crocodile-reversed tarsus remains unknown. If the crocodile-normal tarsus was ancestral to the crocodile-reversed tarsus, then a crocodile-normal tarsus could have been present in primitive ornithosuchids, and the presence of a crocodile-normal tarsus would not bar *Gracilisuchus* from the Ornithosuchidae. Thus, in order to use the structure of the tarsus as a basis for interpreting the interrelationships of archosaurs, it is necessary to obtain a more precise understanding of both the origin of the crocodile-reversed tarsus and the phylogenetic position of *Gracilisuchus.*

THE CROCODILE-NORMAL TARSUS

In extant crocodiles, five elements are present in the tarsus: the astragalus, the calcaneum, and the second to fourth distal tarsals.

The astragalus (Fig. 1C-D) supports the tibia and contacts the fibula by articular surfaces that almost completely cover the proximal surface of the bone. Anteriorly, the astragalus has a strongly covex surface that articulates with the proximal end of the first two metatarsals and the medial surface of the second and third distal tarsals. Above this, the anterior face of the astragalus is formed by a concave area covered by finished bone. Laterally, a distinctive articular surface for the calcaneum is present. This is divisible into two separate areas. The ventral area has the shape of a portion of a

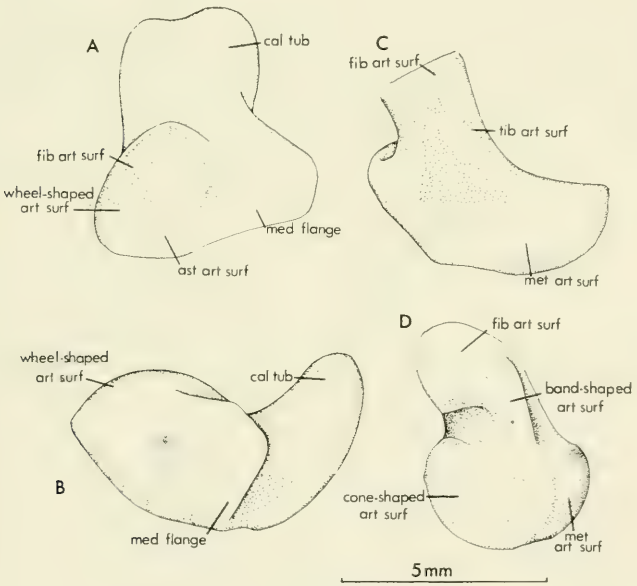


Figure 1. The right astragalus and calcaneum of *Caiman sclerops*. A) calcaneum in proximal view; B) calcaneum in medial view; C) astragalus in dorsal view; D) astragalus in medial view.

Abbreviations: band-shaped art surf, band-shaped articular surface; cal tub, calcaneal tuber; cone-shaped art surf, cone-shaped articular surface; fib art surf, fibular articular surface; med flange, medial flange; met art surf, metatarsal articular surface; tib art surf, tibial articular surface; wheel-shaped art surf, wheel-shaped articular surface; ast art surf, astragalar articular surface.

cone, its apex forming the tip of the laterally directed peg. Dorsal to this, a notch in the lateral edge of the astragalus leads to a band-shaped articular surfce. These two areas meet along a ridge that terminates on the tip of the lateral peg.

The calcaneum (Fig. 1A-B) has three characteristic areas: a dorsal area that has the form of a portion of a wheel, a medially directed flange that underlies the astragalus, and a posteriorly directed tuber. The medial half of the wheel-shaped articular surface fits in the notch on the lateral edge of the astragalus and is overlapped by the astragalus. The lateral half supports the fibula. The fibular and astragalar surfaces are differentiated by a slight change in the curvature of the articular surface. The medially directed flange articulates behind the cone-shaped articular surface of the astragalus. The calcaneal tuber extends across the full width of the bone. The distal end of the tuber is expanded and has a vertical groove in which lie tendons of the long pedal flexors. Anterodistally, the calcaneum as a flat articular surface that abuts the fourth distal tarsal.

A crocodile-normal tarsus is present in the Rauisuchidae (Krebs, 1965, 1973; Sill, 1974), the Aetosauridae (Sawin, 1947; Walker, 1961; Bonaparte, 1971; Sill, 1974), and *Gracilisuchus* Bonaparte, 1975b). A crocodile-normal calcaneum from the uppermost Lower or lowermost Middle Triassic was figured by Young (1964, Fig. 60) and attributed to *Wangisuchus*.

The astragalus in these pseudosuchians, where known, differs from that of crocodiles in having more extensive development of finished bone on its anterior face and in the proportions of the articular surfaces, the metatarsal articular surface being narrower mediolaterally in most genera, as in *Gracilisuchus* (Fig. 4B). The proportions of the calcaneum also show some variation, the calcaneal tuber of aetosaurs being considerably broader than in crocodiles and other pseudosuchians (Sawin, 1947). Despite this variation, the structure of the joint between the astragalus and calcaneum is like that of crocodiles.

THE TARSUS OF *CHASMATOSAURUS*

The tarsus of the early proterosuchid *Chasmatosaurus*[1] (Fig. 2) is primitive in the presence of a separate astragalus and centrale, and

the retention of a foramen between the astragalus and calcaneum. However, comparison with an eosuchian tarsus, such as that of a tangasaurid (Fig. 3), demonstrates that a number of derived features are present. The articular surface between the astragalus and calcaneum in eosuchians is flat and forms a straight line when the tarsus is seen in dorsal view. In *Chasmatosaurus,* the portion of the articular surface proximal to the perforating foramen is inclined relative to the distal portion, with the astragalus overlying the calcaneum. The articular surface between the astragalus and calcaneum is a complex concave-convex joint. The portion of the articular surface distal to the perforating foramen is a ball and socket joint, with the socket on the calcaneum. Proximal to the perforating foramen, a concave-convex joint is also present, but the concavity is on the astragalus. The proximal edge of the calcaneum is not preserved in *Chasmatosaurus vanhoepeni*, but in the

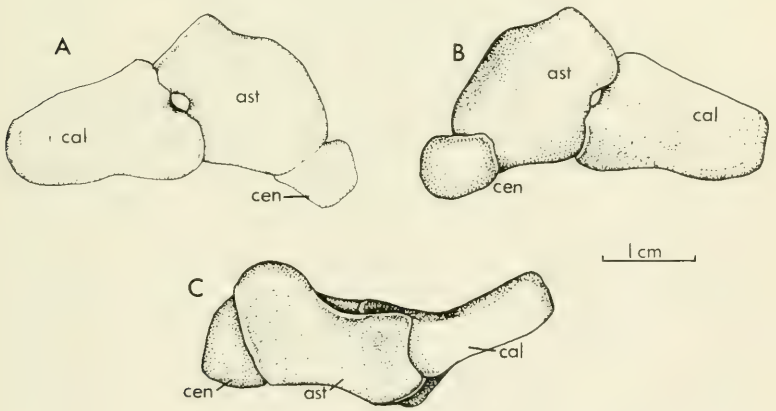


Figure 2. The tarsus of *Chasmatosaurus vanhoepeni.* Left calcaneum, astragalus, and centrale in A) ventral, B) dorsal, and C) proximal views. Drawing based on cast of NM C3016, Nasionale Museum, Bloemfontein.

Abbreviations: ast, astragalus; cal, calcaneum; cen, centrale.

[1]Following Charig and Sues (1976), *Proterosuchus* is considered a nomen dubium, and the remaining proterosuchid material from South Africa is referred to the genus *Chasmatosaurus.*

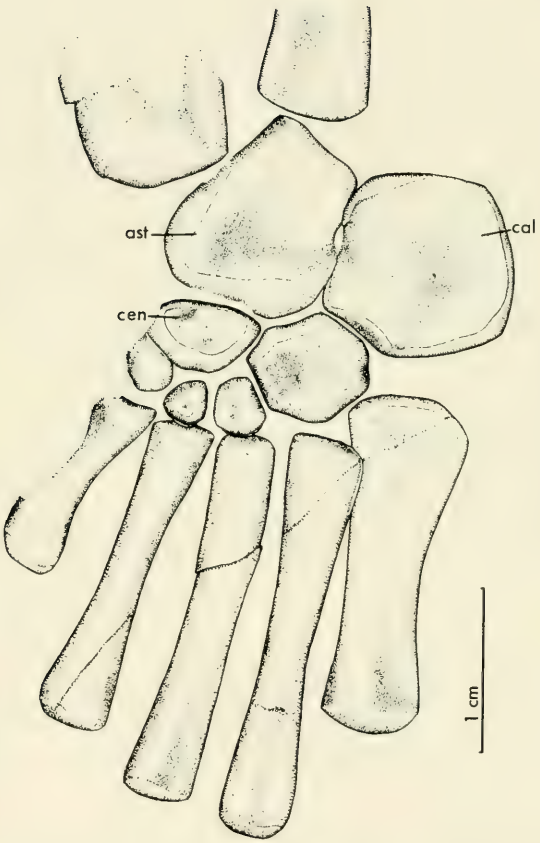


Figure 3. The left tarsus of *Hovasaurus,* a tangasaurid eosuchian, in dorsal view. Drawn from cast of MNHN 1925-5-61, National Museum of Natural History, Paris.

Abbreviations: ast, astragalus; cal, calcaneum; cen, centrale.

calcaneum of *Chasmatosaurus yuani* illustrated by Young (1936, Fig. 9D) the convexity of the calcaneal surface is seen to continue laterally to form a dorsoventrally convex fibular articular surface, as it does in the early rhynchosaur *Noteosuchus* (Fig. 6A).

The calcaneum has been modified from the primitive platelike condition by the development of a laterally extending tuber. The distal edge is thin, and a thickened medial buttress extends transversely across the bone to the expanded cartilage-covered lateral edge. Judging from Young's illustration of the calcaneum of *Chasmatosaurus yuani,* the proximal edge was covered by unfinished bone, as it is in the early rhynchosaur *Noteosuchus* (Fig. 6A).

The centrale has shifted its position so that it is now located laterally, rather than distally, to the astragalus. It may aid in support of the tibia.

Cruickshank (1972), based on the similarity of the tarsus of *Chasmatosaurus* and early rhynchosaurs and the presence in both of a downturned premaxilla, suggested that *Chasmatosaurus* was a carnivorous rhynchocephalian. If the proterosuchian tarsus was restricted to these animals, it would suggest that *Chasmatosaurus* is phylogenetically a rhynchosaur and thus would bring into question the validity of using the proterosuchian tarsus as the primitive archosaur pattern. However, a number of additional groups of diapsid reptiles have a tarsus that, in so far as comparison is possible, is like that of *Chasmatosaurus.* The tarsus of *Prolacerta* (Gow, 1975, Fig. 33) shows all the advanced features seen in *Chasmatosaurus* and early rhynchosaurs. As would be expected, the aquatic members of the Prolacertiformes show a decrease in the ossification of the tarsus. Despite this, mature specimens of *Tanystropheus* (Wild, 1973; Fig. 75) and *Macrocnemus* (Peyer, 1937; Pl. 56, Fig. 2) show the diagnostic features of a laterally directed dorsoventrally compressed tuber on the calcaneum, and a complex concave-convex articulation between the astragalus and calcaneum. A proterosuchian tarsus is also seen in *Protorosaurus* from the Permian of Europe (von Meyer, 1856, Pl. 9), and *Trilophosaurus* from the Triassic of Texas (Fig. 4).

At first glance, this assemblage of reptiles seems to be an unnatural one, bringing together animals with markedly different adaptations and skull configurations. However, a more detailed consideration shows that this assemblage is not as artificial as first

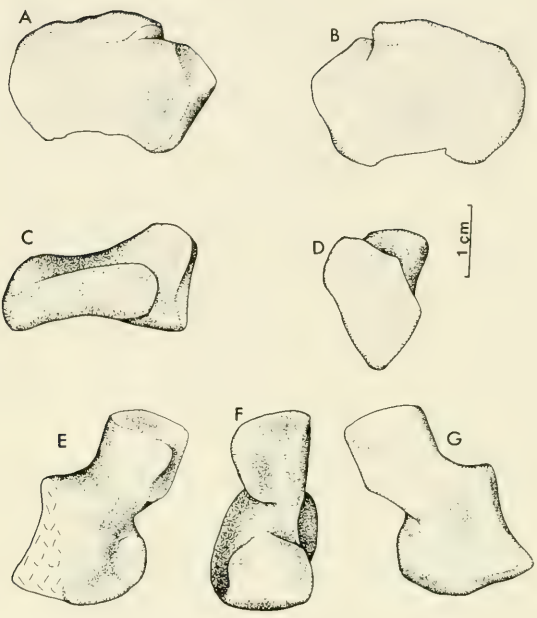


Figure 4. The right astragalus and calcaneum of *Trilophosaurus*. Calcaneum in A) ventral, B) dorsal, C) proximal, and D) distal views; astragalus in E) ventral, F), medial, and G) dorsal views. Calcaneum: specimen TMM 31025-258; astragalus: specimen TMM 31025-259, Texas Memorial Museum.

appears. *Prolacerta* and *Protorosaurus* have long been recognized as being closely related (Camp, 1945; Watson, 1958). Romer (1956) denied the presence of such a relationship, choosing to place *Protorosaurus* in the Euryapsida because of the presumed presence of a solid cheek. However, as noted by Chatterjee (1980), much uncertainty about the structure of the skull of *Protorosaurus* exists. Details of the skull and postcranial skeleton that are known for certain are similar to *Prolacerta,* and Chatterjee unites these genera in the suborder Prolacertiformes. Gow (1975) concluded on the basis of evidence from the skull of *Prolacerta* that the Prolacertiformes are related to archosaurs.

The remaining groups in this assemblage, rhynchosaurids and trilophosaurids, have highly specialized skulls that could be derived from any primitive diapsid, so the skull neither supports nor negates a relationship between these groups and the archosaur-protoro-

saurid-prolacertid group. Postcranially, both trilophosaurids and rhynchosaurids are less specialized, and a similarity in the structure of their postcranial skeletons and the postcranial skeleton of some members of the archosaur-protorosaurid-prolacertid group has been noted (Gregory, 1945; Carroll, 1976), although it is not certain whether these represent derived features or primitive features widespread in diapsid reptiles.

Thus, there seems to be no need to hypothesize a multiple origin of the proterosuchian tarsus. If rhynchosaurs, prolacertiformes, prolacertids, trilophosaurids, and archosaurs are a natural group, the proterosuchian tarsus could have originated only once. One implication of this is that the proterosuchian tarsus is the primitive archosaur tarsus and is the ultimate structural ancestor of the various kinds of tarsi seen in advanced archosaurs. In some cases, an intermediate structural complex may have been present, but, as shown by Cruickshank (1979), the proterosuchian tarsus was probably the direct structural antecedent of the crocodile-normal tarsus. It is useful to identify the structural changes that would have occurred during this transition before considering the structure and origin of the crocodile-reversed tarsus.

ORIGIN OF THE CROCODILE-NORMAL TARSUS

As recognized by Cruickshank (1979), the astragalus-centrale unit of the proterosuchian tarsus is directly comparable to the astragalus of the crocodile-normal tarsus (Fig. 5). The area distal to the perforating foramen is homologous to the cone-shaped articular surface of the crocodile-normal tarsus, but differs in being smaller and less strongly curved. The area proximal to the perforating foramen is homologous to the dorsal half of the notch on the lateral edge of the crocodile-normal astragalus, the main difference being that in the proterosuchian tarsus this surface is separated from the distal surface by finished bone.

The calcaneum of the crocodile-normal and proterosuchian tarsi (Fig. 6) differs in the orientation of the calcaneal tuber; in the proterosuchian tarsus, this is directed laterally, while in the crocodile-normal tarsus, this is directed more posteriorly. If the calcaneal tuber of the proterosuchian tarsus were oriented so that it extended posteriorly, the articular surface for the fibula and astragalus would be oriented along the long axis of the bone rather

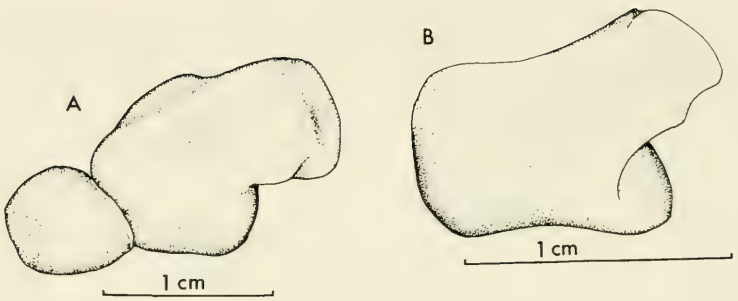


Figure 5. The left astragalus of the proterosuchian and crocodile-normal tarsus in anterior view. A) astragalus and centrale of *Noteosuchus;* B) astragalus of *Gracilisuchus.* Not drawn to scale. *Noteosuchus* based on cast of Albany Museum 3591. *Grasilisuchus* based on cast of specimen in collection of Paleontologia Vertebrados de la Fundacion M. Lillo.

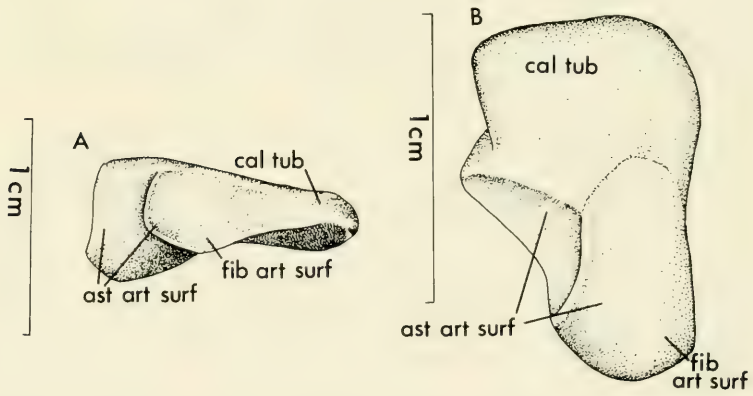


Figure 6. The left calcaneum of the proterosuchian and crocodile-normal tarsus. A) calcaneum of *Noteosuchus;* B) calcaneum of *Gracilisuchus.*

Abbreviations: ast art surf, astragalar articular surface; cal tub, calcaneal tuber; fib art surf, fibular articular surface.

than across it. A simple enlargement of the articular surface, together with the extension of the proximal portion of the astragalar articular surface onto the medial edge of the perforating foramen, would form the wheel-shaped articular surface of the crocodile-normal calcaneum. An enlargement of the ventral half of the articular surface for the astragalus would form the medial flange of the crocodile-normal calcaneum.

Thus structurally, the proterosuchian tarsus is an excellent ancestor of the crocodile-normal tarsus. The mechanical changes involved in this transition were probably minor, since, as noted by Thulborn (1980), the joint between the astragalus and calcaneum was probably movable in the proterosuchian tarsus.

THE CROCODILE-REVERSED TARSUS

The crocodile-reversed tarsus is best known in the ornithosuchid *Riojasuchus* (Bonaparte, 1971, 1975b). Dorsally, the calcaneum (Fig. 7B) has an articular surface that is convex both mediolaterally and proximodistally. This surface supports the fibula along its lateral edge and the astragalus along its medial edge. These are exactly the relationships of the wheel-shaped articular surface of the crocodile-normal tarsus (Fig. 8A-B). The major difference is that the medial edge of this area is hypertrophied in *Riojasuchus* to form a medially directed process. This process is functionally equivalent to the ventral flange of the crocodile-normal calcaneum in that it underlies the astragalus (Fig. 8C-D). Consequently, it is not surprising that the ventral flange or an homologous area is not present in the crocodile-reversed calcaneum. The absence of the ventral flange is associated with a reduction in the width of the calcaneal tuber; in the crocodile-reversed tarsus, the calcaneal tuber does not extend the full width of the bone. In addition, the tuber of the crocodile-reversed tarsus is distinctive in that its distal end curves medially and is without a groove for the tendon of the gastrocnemial muscles.

The differences in structure of the astragalus of the crocodile-normal and crocodile-reversed tarsus correspond to the differences in structure of the calcaneum: the hypertrophy of the medial edge of the wheel-shaped articular surface is associated with the elongation of the overlying portion of the astragalus, and the loss of the ventral flange is associated with the loss of the cone-shaped articular surface.

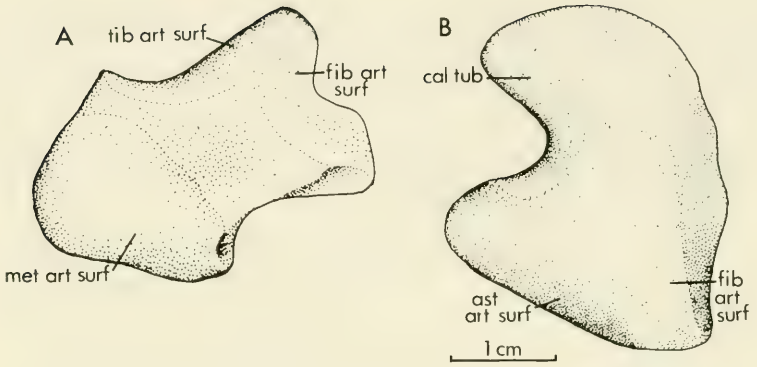


Figure 7. The left astragalus and calcaneum of the crocodile-reversed tarsus. A) Astragalus and B) calcaneum of *Riojasuchus*. Drawn from cast of PVL 3827, Paleontologia Vertebrados de la Fundacion M. Lillo.

Abbreviations: ast art surf, astragalar articular surface; cal tub, calcaneal tuber; fib art surf, fibular articular surface; met art surf, metatarsal articular surface; tib art surf, tibial articular surface.

From this comparison, it can be seen that the crocodile-normal tarsus is a plausible ancestor of the crocodile-reversed tarsus. The major changes involved in such a transition would be the medial elongation of the wheel-shaped articular surface of the calcaneum and the loss of the ventral flange. Derivation of the crocodile-reversed tarsus directly from the primitive archosaur tarsus is also possible. However, derivation of the crocodile-normal tarsus from the crocodile-reversed tarsus can be discounted as being improbable since it would involve the redevelopment of the ventral flange, a structure that is present in the crocodile-normal tarsus and the primitive archosaur tarsus but absent in the crocodile-reversed tarsus.

Given this relationship of the crocodile-normal and crocodile-reversed tarsi, the structure of the tarsus cannot be used to exclude *Gracilisuchus* from the Ornithosuchidae. Rather, the systematic position of *Gracilisuchus* has implications for the evolution of the tarsus. If *Gracilisuchus* is a true ornithosuchid, the crocodile-normal tarsus must have given rise to the crocodile-reversed tarsus, and the structure of the tarsus has little real phylogenetic significance. If however, *Gracilisuchus* is not an ornithosuchid, the crocodile-reversed tarsus may have originated independently from

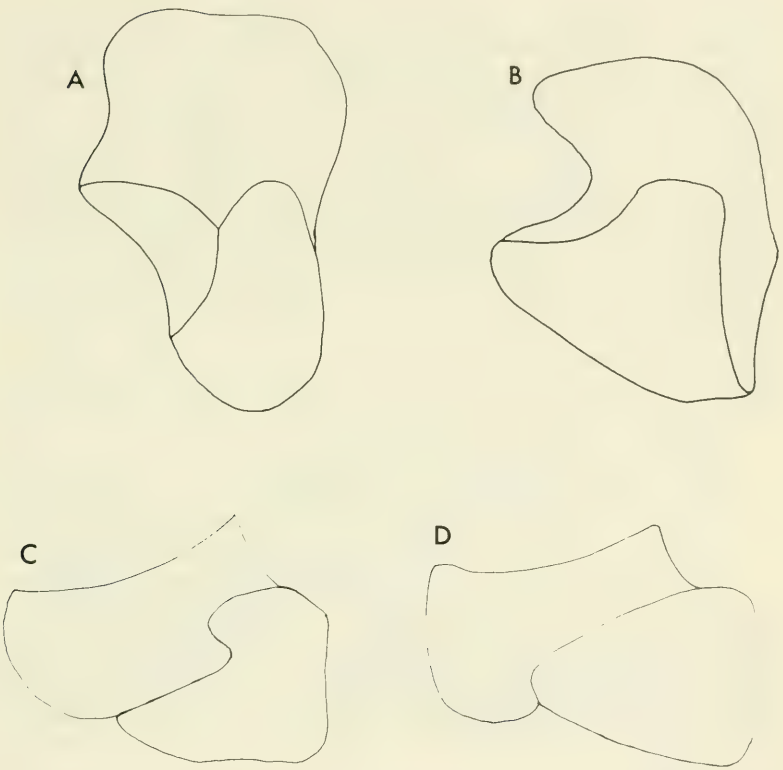


Figure 8. The left calcaneum of the crocodile-normal and crocodile-reversed tarsi. A) crocodile-normal calcaneum of *Gracilisuchus* in proximal view; B) crocodile-reversed calcaneum of *Riojasuchus* in proximal view; C) section through an articulated crocodile-normal astragalus and calcaneum; D) section through an articulated crocodile-reversed astragalus and calcaneum. Not drawn to scale.

the proterosuchian tarsus, and the presence of the crocodile-reversed tarsus can be used as the defining feature of some taxonomic group. Thus it is necessary to reconsider the relationships of *Gracilisuchus*.

THE RELATIONSHIPS OF *GRACILISUCHUS*

The skull of *Gracilisuchus* was reconstructed by Romer (1972) on the basis of MCZ 4117, a complete, three dimensional skull. One of

the unusual features seen in this skull is a small lower temporal opening. However, other material, particularly MCZ 4116 and MCZ 4118, show that MCZ 4117 has been slightly crushed and the quadratojugal and squamosal have been displaced. In MCZ 4116, the preorbital bar is slender and the antorbital opening is larger than in MCZ 4117 (Fig. 9A). In MCZ 4118, the postorbital bar is tall and slender, the quadratojugal and squamosal are separated from the postorbital, and the lower temporal opening is large and rectangular (Fig 9B). Based on these skulls, the arrangement of the temporal region and the height of the face in the reconstruction of the skull of *Gracilisuchus* is modified (Fig. 9B).

Gracilisuchus differs from the advanced ornithosuchids as defined by Bonaparte (1975b) (Fig. 10) in the following features:

1) The antorbital fenestra is rectangular in *Gracilisuchus* and is triangular in the advanced ornithosuchids.
2) The ventral border of the orbit is round in *Gracilisuchus,* and a distinct antorbital ramus of the jugal is not present. In the advanced ornithosuchids, a distinct preorbital ramus of the jugal is present; this is close to the postorbital ramus at its base, so the ventral margin of the orbit is pointed.
3) The quadratojugal of *Gracilisuchus* is a tall, slender element that extends nearly the full height of the lower temporal opening. In the advanced ornithosuchids, the quadratojugal is broader and is limted to the ventral half of the lower temporal opening.
4) The upper tooth row is complete, and all the teeth of the lower jaw fit inside the upper teeth row in *Gracilisuchus.* In advanced ornithosuchids, a gap is present between the anterior tooth of the maxilla and the posterior tooth of the premaxilla, with the anterior one or two dentary teeth passing lateral to the maxilla in this gap.
5) In *Gracilisuchus,* the lower temporal fenestra is rectangular, and no anterior inflection of the quadratojugal and squamosal is present. In the advanced ornithosuchids, a large anterior inflection of the quadratojugal and squamosal results in the presence of an L-shaped lower temporal fenestra.
6) In *Gracilisuchus,* the squamosal has a peculiar, posteriorly concave flange on its dorsal end. No such flange is present in the advanced ornithosuchids.

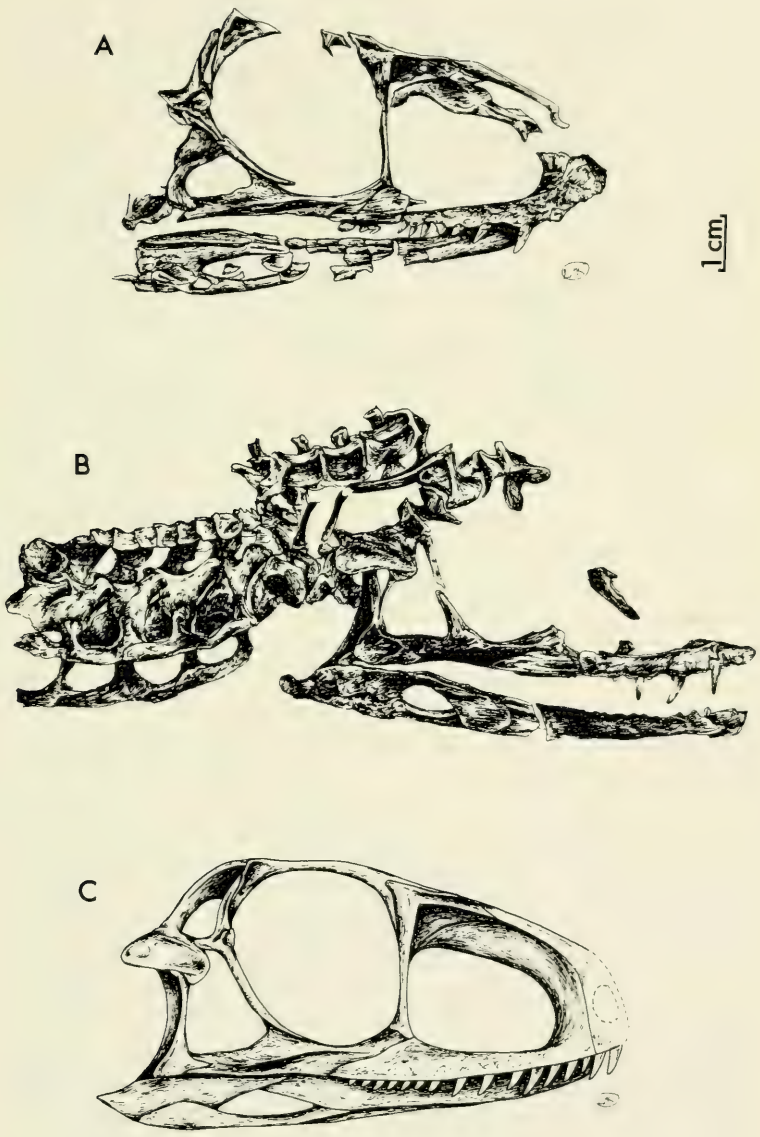


Figure 9. The skull of *Gracilisuchus*. A) specimen drawing of MCZ 4116; B) specimen drawing of MCZ 4118; C) reconstruction of skull.

7) In *Gracilisuchus,* the posterior end of the dentary extends dorsal to the mandibular fenestra. In the advanced ornithosuchids, the posterior end of the dentary is forked, with one branch extending dorsal and one branch extending ventral to the lateral mandibular fenestra.
8) In *Gracilisuchus,* the splenial forms the ventral margin of the jaw along the posterior half of the dentary. In the advanced ornithosuchids, the splenial is restricted to the inner surface of the jaw.
9) In *Gracilisuchus,* the cervical vertebrae are not keeled. In the advanced ornithosuchids, the cervical vertebrae, where known (*Riojasuchus* and *Ornithosuchus*), are keeled.
10) In *Gracilisuchus,* there are two pairs of dermal scutes per vertebra in the cervical region of the vertebral column. In the advanced ornithosuchids, where known (*Ornithosuchus* and *Riojasuchus*), there is one pair of scutes per vertebra.

This list of differences between *Gracilisuchus* and the advanced ornithosuchids shows that the advanced ornithosuchids are more similar to each other than to *Gracilisuchus.* But these features by themselves do not demonstrate that *Gracilisuchus* is not an ornithosuchid; *Gracilisuchus* occurs much earlier in time than the advanced ornithosuchids, so the differences may represent successive grades of evolution in a single radiation. In order to be used phylogenetically, it is necessary to determine which of the character-states represent derived features. *Euparkeria* (Fig. 10D), the oldest known pseudosuchian, had traditionally been considered to be the structural ancestor of later pseudosuchians and thus can be used as the outgroup in determining which character-states are primitive or advanced.

Features that are shared by *Gracilisuchus* and *Euparkeria*, and thus can be considered primitive, are the presence of a complete upper tooth row with all the dentary teeth fitting inside the upper tooth row, the shape of the lower temporal fenestra, and the shape of the antorbital fenestra (features 1, 4, and 5 in the above list). In all other features, *Euparkeria* is like the advanced ornithosuchids and unlike *Gracilisuchus:* the jugal has a well-developed antorbital process, and the base of this is near the postorbital process; the squamosal is without the peculiar posteriorly concave flange seen in *Gracilisuchus*; the posterior end of the dentary is forked, with a branch above and a branch below the lateral mandibular fenestra;

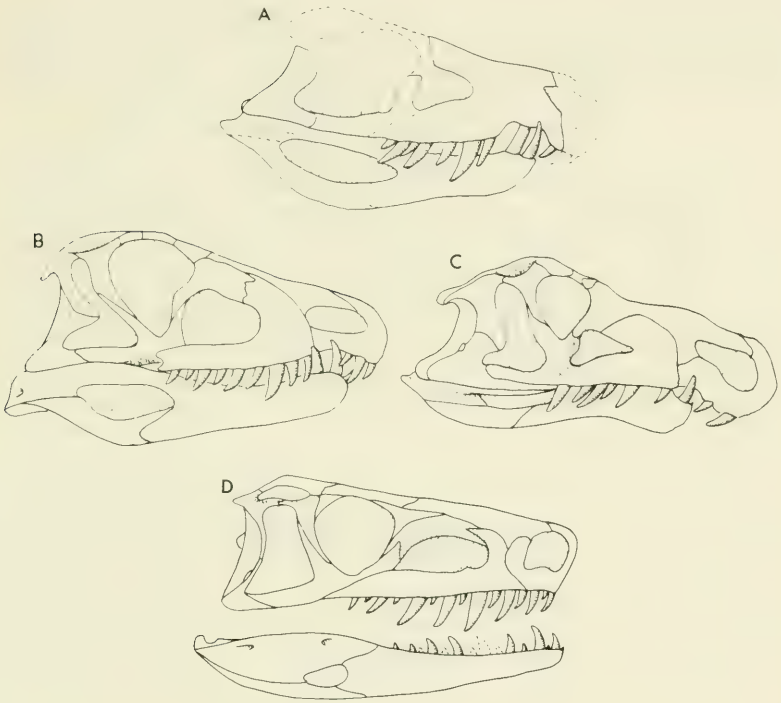


Figure 10. The skulls of the advanced ornithosuchids and *Euparkeria.* A) *Venaticosuchus;* B) *Ornithosuchus;* C) *Riojasuchus;* D) *Euparkeria.* From Bonaparte, 1975.

the splenial is restricted to the internal surface of the lower jaw; the cervical vertebrae are keeled; and one pair of dermal scutes is present per vertebral segment. For these features, the character-state present in the advanced ornithosuchids must be considered primitive, and the *Gracilisuchus* condition derived.

Thus, if an ornithosuchid, *Gracilisuchus* is derived from the ornithosuchid pattern in a way different from the advanced ornithosuchids. Alternatively, *Gracilisuchus* may be a member of a radiation distinct from that of ornithosuchids. This latter possibility is suggested by the presence of some of the derived features of *Gracilisuchus* in *Sphenosuchus, Pseudohesperosuchus,* and *Lewisuchus,* pseudosuchians that are thought to be unrelated to ornithosuchids (Romer, 1972). These features include the tall,

slender quadratojugal, the posterior flange on the squamosal (known in *Pseudohesperosuchus* and *Sphenosuchus*), and the presence of unkeeled cervical vertebrae (known in *Lewisuchus*).

THE TARSUS OF *EUPARKERIA*

The similarity between ornithosuchids and *Euparkeria* raises the possibility that *Euparkeria* is closely related to the Ornithosuchidae, rather than being a generalized primitive pseudosuchian. Such a relationship is supported by the structure of the tarsus. The astragalus and calcaneum of *Euparkeria* were illustrated by Bonaparte (1975) and Cruickshank (1979). As noted by these authors, these elements are directly comparable to those of the crocodile-reversed tarsus (Fig. 11). The dorsal portion of the articular surface of the calcaneum is divisible into two areas, a narrow area along the lateral edge of the bone that would have articulated with the fibula, and a medial area that would have articulated with the astragalus. The astragalar area is in the shape of a portion of a cone with its apex directed medially. No area comparable to the ventral flange of the crocodile-normal tarsus is present. The calcaneal tuber is directed posteriorly and is narrow.

Thus the calcaneum of *Euparkeria* is similar to the crocodile-reversed tarsus in all the features by which the crocodile-normal and crocodile-reversed tarsi differ. Of special importance is the absence of an area homologous to the ventral flange of the astragalus of the crocodile-normal tarsus. As was argued above, the absence of this area prevents derivation of a crocodile-normal tarsus from a crocodile-reversed tarsus without the redevelopment of a lost structure. On this basis, *Euparkeria* can be considered to be more closely related to the ornithosuchids than to any pseudosuchian with a crocodile-normal tarsus.

THE TARSUS OF *ERYTHROSUCHUS*

An additional problem to be considered is the relationship of *Erythrosuchus*. Sill (1974) showed that a striking similarity exists between the skull of *Erythrosuchus* and rauisuchids, so that a relationship between these two groups is probable. Cruickshank (1978, 1979), however, felt that the tarsus of *Erythrosuchus* was most similar to that of Euparkeria, and placed *Erythrosuchus* with *Euparkeria* and the ornithosuchids in his Ornithosuchoidea.

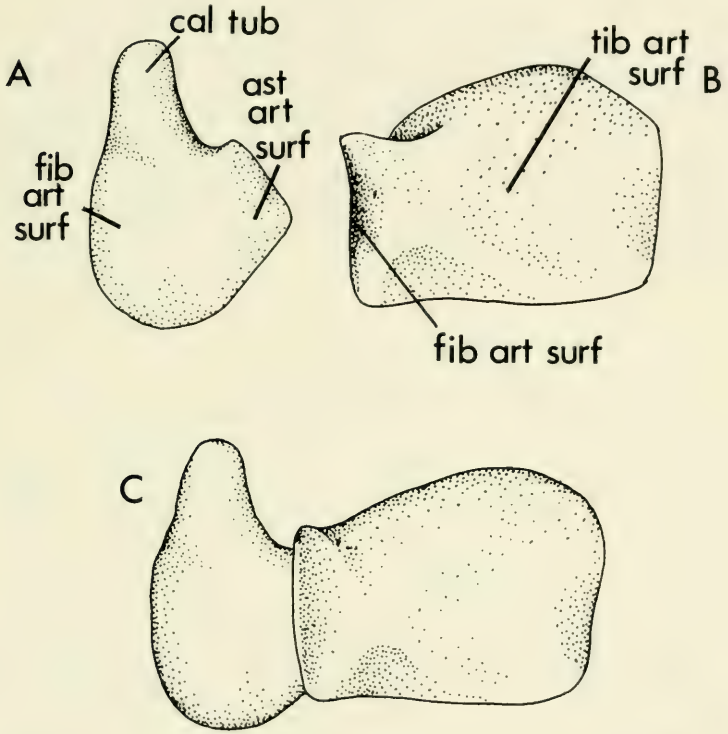


Figure 11. The right astragalus and calcaneum of *Euparkeria*. A) astragalus; B) calcaneum; and C) astragalus and calcaneum in articulation. A and B from Bonaparte (1975), C based on drawings of South African Museum specimen SAM 6049 made by J. Bonaparte.

Abbreviations: ast art surf, astragalar articular surface; cal tub, calcaneal tuber; fib art surf, fibular articular surface; tib art surf, tibial articular surface.

A general similarity between the tarsus of *Erythrosuchus* and *Euparkeria* is present, but this can be attributed to the poor ossification of the bones. More fundamental is the similarity between the tarsus of *Erythrosuchus* and *Chasmatosaurus*. A comparison of the calcaneum of these two animals (Fig. 12) shows that the calcaneal tuber extends laterally, has thin proximal and distal edges, and has a thickened medial buttress that extends across the tuber to an expanded cartilage-covered lateral edge. The poor ossification of the astragalus of *Erythrosuchus* obscured the structure of the articulation between the astragalus and calcaneum,

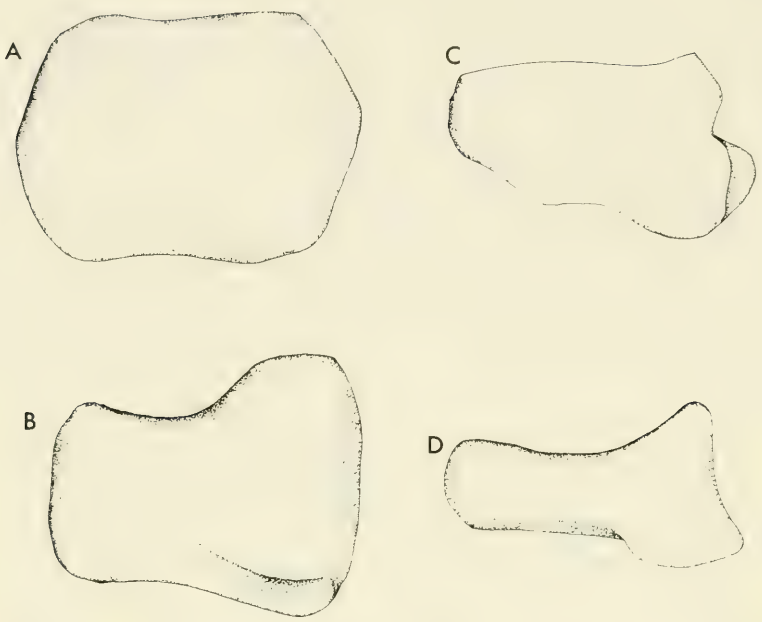


Figure 12. The left calcaneum of *Erythrosuchus* in A) ventral, and B) distal views; and *Chasmatosaurus* in C) ventral, and D) distal views. *Erythrosuchus* drawing based on cast of Bernard Price Institute F. 2069/M 405, *Chasmatosaurus* drawing based on cast of NM C 3016, Nasionale Museum, Bloemfontein.

although Cruickshank (1978) identifies a perforating foramen, a primitive feature that is also present in *Chasmatosaurus*.

Thus the tarsus of *Erythrosuchus* is best considered a poorly ossified proterosuchian tarsus. A reduction of ossification is commonly seen in aquatic animals, and probably reflects an adaptation for an aquatic habitat, rather than the development of a mechanically distinct structural complex. A fully terrestrial erythrosuchid would, therefore, be expected to have a tarsus like that of *Chasmatosaurus*. Since this kind of tarsus is the structural ancestor of the crocodile-normal tarsus, the structure of the erythrosuchid tarsus neither supports nor negates a relationship between erythrosuchids and rauisuchids. If a relationship between erythrosuchids and rauisuchids is accepted on the basis of similarities in the skull, it is necessary to assume that the crocodile-normal tarsus originated after the origin of this radiation of thecodonts, and therefore the tarsus cannot be used as the defining feature of the group.

SUMMARY

A summary of the relationships suggested above may be made in the form of a phylogenetic diagram (Fig. 13). According to this phylogeny, many of the higher taxa of diapsid reptiles are artificial assemblages, and major modifications of reptilian classification are necessary to accurately reflect reptilian relationships. It would, however, be useful to test these relationships through examination of other structural complexes before making the necessary changes.

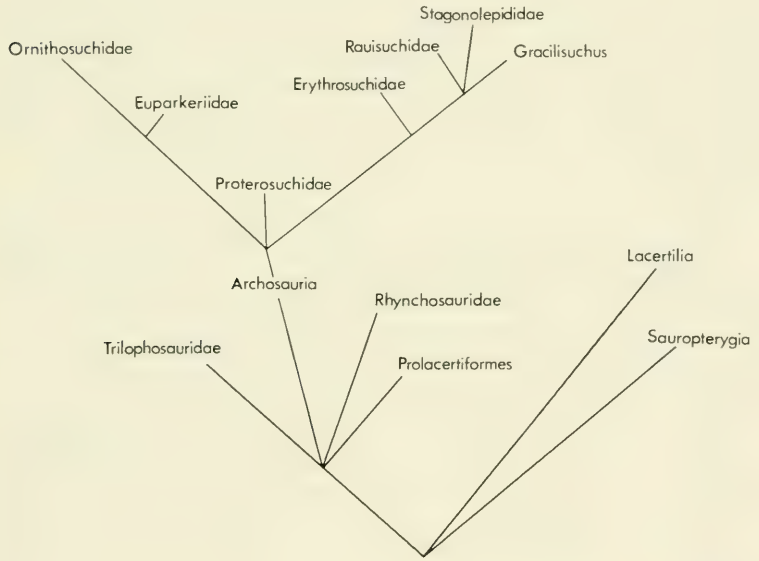


Figure 13. The interrelationships of thecodonts.

ACKNOWLEDGMENTS

I would like to thank Dr. R. L. Carroll, at whose suggestion this project was undertaken. For reading the manuscript and making many useful suggestions, I thank Hans Dieter Sues, Museum of Comparative Zoology, Harvard University; Michael Parrish, University of Chicago; Dr. Sankar Chatterjee, Texas Tech University; and Robert Long and Dr. S. Welles, University of California,

Berkeley. I also thank Lillian Maloney, who proofread the manuscript. Figure 9 was drawn by Linda Krause. Publication costs of this study were covered in part by a grant from the Wetmore Colles Fund.

LITERATURE CITED

BONAPARTE, J. F. 1971. Los tetrapodos del sector superior de la formation Los Colorados, La Rioja, Argentina. Opera Lilloana, **22:** 1–183.

———. 1975a. Nuevos materials de *Lagosuchus talampayensis* Romer (Thecodontia-Pseudosuchia) y su significade en el origen de los Saurischia. Acta Geol. Lilloana, **13:** 5–87.

———. 1975b. The family Ornithosuchidae (Archosauria: Thecodontia). Colloques int. Cent. Natn. Rech. Scient. No. 218, pp. 485–506.

CAMP, C. L. 1945. *Prolacerta* and the protorosaurian reptiles. Am. J. Sci., **243:** 17–32, 84–101.

CARROLL, R. L. 1976. *Noteosuchus,* the oldest known rhynchosaur. Ann. S. Afr. Mus., **72:** 37–57.

CHARIG, A. J., AND H. -D. SUES. 1976. Proterosuchia, pp. 11–39. *In* A. J. Charig, B. Krebs, H. -D. Sues, and F. Westphal, Handbuch der Palaoherpetologie, 13, Stuttgart and Portland, Gustav Fischer, 137 pp.

CHATTERJEE, S. 1978. A primitive parasuchid (phytosaur) reptile from the Upper Triassic Maleri Formation of India. Paleontology, **21:** 83–127.

———. 1980. Malerisaurus, a new eosuchian reptile from the late Triassic of India. Phil. Trans. Roy. Soc. Lond. (B). **291:** 163–200.

CRUICKSHANK, A. R. I. 1972. The proterosuchian thecodonts, 89–119. *In* K. A. Joysey, and T. S. Kemp (eds.), Studies in Vertebrate Evolution: Essays Presented to Dr. F. R. Parrington F. R. S. Edinburgh, Oliver and Boyd, 284 pp.

———. 1978. The pes of *Erythrosuchus africanus* Broom. J. Linnean Soc. (Zool.), **62:** 161–178.

———. 1979. The ankle joint in some early archosaurs. S. Afr. J. Sci., **75:** 168–178.

GOW, C. E. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. Paleontol. Afr., **18:** 89–131.

GREGORY, J. T. 1945. Osteology and relationships of *Trilophosaurus.* U. of Texas Publ. No. 4401, pp. 273–359.

KREBS, B. 1963. Bau und Function des Tarsus eines Pseudosuchiers aus der Trias des Monte San Giorgio (Kanton Tessin, Schweiz.). Paläontol. Z., **37:** 88–95.

———. 1965. *Tictinosuchus ferox* nov. gen., nov. sp. Ein neuer Pseudosuchier aus der Trias des Monte San Giogio. Schweiz. Paläontol. Abh., **81:** 1–140.

———. 1973. Der Tarsus von *Rauisuchus* (Pseudosuchia, Mittel Trias). Mitt. Bayer. Staatsamml. Paläontol. Hist. Geol., **13:** 95–101.

PEYER, B. 1937. Die Triasfauna der Tessiner Kalkalpen, XII *Macrocnemus bassanii* Nopsca. Schweiz. Paläontol. Abh., **59:** 1–140.

ROMER, A. S. 1956. The Osteology of the Reptiles. Chicago, University of Chicago Press, 772 pp.

_____. 1971. The Chañares (Argentina) Triassic reptile Fauna X. Two new but incompletely known long-limbed pseudosuchians. Mus. Comp. Zool., Breviora No. 378, pp. 1–10.

_____. 1972. The Chañares (Argentina Triassic Reptile Fauna, XIII. An early ornithosuchid pseudosuchian, *Gracilisuchus stipaniaicorum,* gen. et sp. nov. Mus. Comp. Zool., Breviora No. 389, pp. 1–24.

SAWIN, H. J. 1947. The pseudosuchian reptile *Typothorax meadei.* J. Paleontol., **21:** 201–238.

SILL, W. D. 1974. The anatomy of *Saurosuchus galilei* and the relationships of the rauisuchid thecodonts. Bull. Mus. Comp. Zool., **146:** 317–362.

THULBORN, R. A. 1980. The ankle joints of archosaurs. Alcheringa, **4:** 241–261.

VON MEYER, H. 1856. Zur Fauna der Vorwelt, Saurier aus dem Kupferschiefer der Zechstein-Formation. Frankfut-am-main.

WALKER, A. D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis, Dasygnathus* and their allies. Phil. Trans. Roy. Soc. Lond. (B), **244:** 103–204.

_____. 1970. A revision of the Jurassic reptile *Hallopus victor* (Marsh), with remarks on the classification of crocodiles. Phil. Trans. Roy. Soc. Lond. (B), **257:** 323–372.

WATSON, D. M. S. 1958. On *Millerosaurus* and the early history of the sauropsid reptiles. Phil. Trans. Roy. Soc. Lond. (B), **240:** 355–400.

WILD, R. 1973. Die Triasfauna der Tessiner Kalkalpen XXIII. Tanystropheus longobardicus (Bassani) (Neue Ergebnisse). Schweiz. Paläontol. Abh., **95:** , 1–162.

YOUNG, C. C. 1936. On a new *Chasmatosaurus* from Sinckiang. Bull. Geol. Soc. China, **15:** 291–320.

_____. 1964. The pseudosuchians in China. Palaeontol. Sinica, New Ser. C, **19:** 1–205.

MUS. COMP. ZOOL
LIBRARY
MAR 1 8 1985
HARVARD
UNIVERSITY

B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 30 DECEMBER 1981 NUMBER 465

THE STRUCTURE AND RELATIONSHIPS OF THE DROMASAURS (REPTILIA: THERAPSIDA)

DONALD BRINKMAN[1]

ABSTRACT. The dromasaurs are primitive anomodonts that are advanced over the venjukoviamorph grade of evolution in the reduction of the postorbital and zygomatic branches of the jugal, the reduction of the septomaxilla, and the enlargement of the area on the dentary for the insertion of the external mandibular muscle. Derived features that distinguish dromasaurs from dicynodonts are the lack of canines, the presence of a tall, slender postorbital, and the rodlike lower temporal bar. The three known dromasaurs form a structural series showing changes in the proportions of the face, a loss of premaxillary teeth, changes in the curvature of the humerus, and a loss of the ectepicondylar foramen.

INTRODUCTION

Frequently, the earliest representatives of higher taxa include groups that are at a primitive grade of evolution but are, in some features, highly specialized. Within the Therapsida, one such group is the Dromasauria. The first dromasaur to be recognized, *Galechirus,* was initially considered to be more primitive than any other therapsid known at that time (Broom, 1907). Later, two additional genera, *Galepus* and *Galeops,* were recognized, with *Galeops* being considered sufficiently distinct to be placed in its own family, the Galeopsidae (Broom, 1910, 1912). The better understanding of the dromasaur skull provided by these genera showed that they were, in many respects, derived from the primitive therapsid condition, and

[1]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

Broom (1914: 12) suggested that they were "an aberrant group of small primitive therapsids."

While there has been little question of the reality of the group, its relationships have been a matter of much uncertainty. Romer and Price (1940) noted that many of the features that separated dromasaurs from other therapsids were primitive for pelycosaurs of the suborder Edaphosauria, implying that a close relationship existed between the two groups. Later, in a review of therapsid classification, Romer and Watson (1956) suggested that a relationship between dromasaurs and dicynodonts was likely, and placed the dromasauria within the Suborder Anomodontia as an infraorder equal in rank to the Dicynodontia. The possibility that both of these relationships are correct was raised by Olson (1962), who suggested that the therapsids had a multiple origin, with the anomodonts originating from within the Edaphosauria.

Uncertainty about the relationships of the dromasaurs is a result of an incomplete understanding of the anatomy of the genera comprising the group. Although much of the skeleton is preserved, the original material consists of natural casts, so that Broom was able to determine little more than the outlines of the bones. Recognizing these problems, it was decided to reexamine the specimens studied by Broom using the methods developed for the study of specimens preserved as natural casts by Baird (1951, 1955) and Carroll (1976), in which latex peels of the specimens provide a positive image of the bones. Because it is the most completely preserved of the dromasaurs, *Galeops* will be described first.

GALEOPS

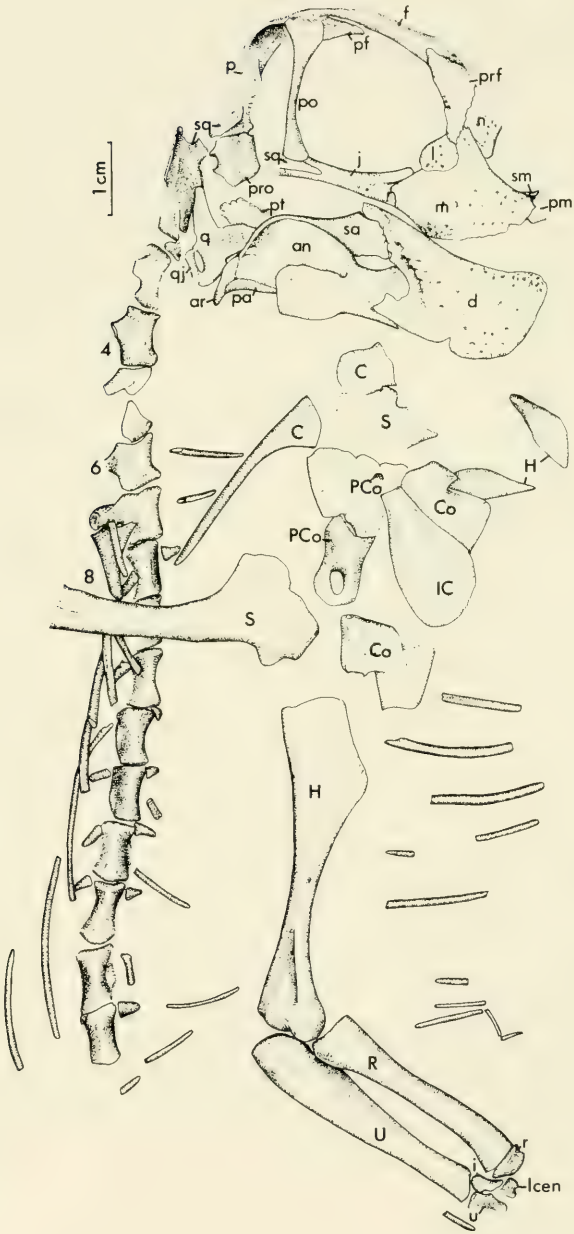
Materials and Methods: Galeops is represented by a single species, *Galeops whaitsi,* and by a single specimen, AMNH 5536, that comes from the *Tapinocephalus* zone of South Africa (Kitching, 1977). It consists of the impressions of the skull and the front half of the postcranial skeleton in a fine-grained sandstone. Both part and counterpart are present. Latex peels of the specimen provided a positive image of the skeleton, and in some cases, it was possible to cast the two halves of the individual elements and join them together to give three-dimensional replicas of the original bone.

Skull Roof: The skull of *Galeops* (Figs. 1–5) is small for a therapsid, its length from snout to quadrate being 55 mm. The orbits and external narial openings are large and face laterally. The face and postorbital regions are short. Sclerotic rings are present. The ventral margin of the postorbital region is deeply emarginated, reducing the zygomatic bar to a slender rod. The posterior edge of the upper temporal opening is folded backwards, providing a large area for the temporal muscles. No such outfolding of the squamosal is present ventral to the zygomatic bar. The occiput slopes forward and grades into the skull roof. A large pineal opening is present at the level of the frontal-parietal suture (Fig. 4). The teeth are reduced in size and are restricted to the maxilla—presumably a horny beak would have been present anteriorly.

Much of the lateral surface of the face is formed by the maxilla. In lateral view, this bone is triangular with its apex directed dorsally. It is sculptured by numerous small pits and grooves, with these being most strongly developed anteriorly. The relationship of the maxilla to the surrounding bones of the face is similar to that of dicynodonts: it articulates with the jugal, lacrimal, and prefrontal posteriorly; the nasal dorsally; and the premaxilla midway below the external narial opening. The contacts of the maxilla with the prefrontal and nasal are strongly interdigitating sutures. The lacrimal appears to overlay the maxilla, with the suture line being straight in external view. The details of the remaining contacts are uncertain.

Ventrally, the maxilla has a well-developed palatal flange that borders the internal narial opening (Fig. 5). Four sockets are present in the left and five in the right maxilla. These increase in size posteriorly from the first to third, with the fourth being about equal in size to the second in the case of the right maxilla. A distinct canine is not present.

A small portion of the lateral surface of the premaxilla is present ventral to the external narial opening. This has a roughened surface like that of the maxilla. Ventrally, the paired premaxillae have large palatal flanges that form a dicynodontlike secondary palate (Fig. 5). The ventral surfaces of these flanges are roughened by numerous posteriorly projecting spicules of bone. A distinct suture separates the two premaxillae from each other.


f
pf
prf
p
po
n
sq
sq
j
l
sm
pm
1 cm
pro
pt
m
q
sa
an
qj
ar
pa
d
4
C
S
C
H
6
PCo
Co
PCo
8
IC
S
Co
H
R
U
r
i
lcen
u

A small septomaxilla spans the premaxilla-maxilla suture (Fig. 1). It has no exposure on the lateral surface of the face. The septomaxilla foramen is a small opening located between the septomaxilla and maxilla.

The nasal has a large exposure on the lateral surface of the face and forms the dorsal half of the posterior margin of the external narial opening. The anterior three quarters of the bone has a roughened pitted texture like that of the maxilla. Posterior to this, the lateral surface of the nasal is smooth.

The lacrimal, in lateral view, appears to be a small subcircular bone fitting between the maxilla, jugal, and prefrontal. The orbital edge of the bone has an internally directed flange, although this is incompletely preserved (Fig. 2).

The jugal is reduced to a slender rodlike bone forming the ventral margin of the orbit and articulating with the postfrontal and squamosal posteriorly and with the maxilla and lacrimal anteriorly. No contribution to the formation of the postorbital or zygomatic bar is made by the jugal. Anteriorly, a well-defined groove is present on the lateral surface of the jugal. This may have been associated with the horny beak.

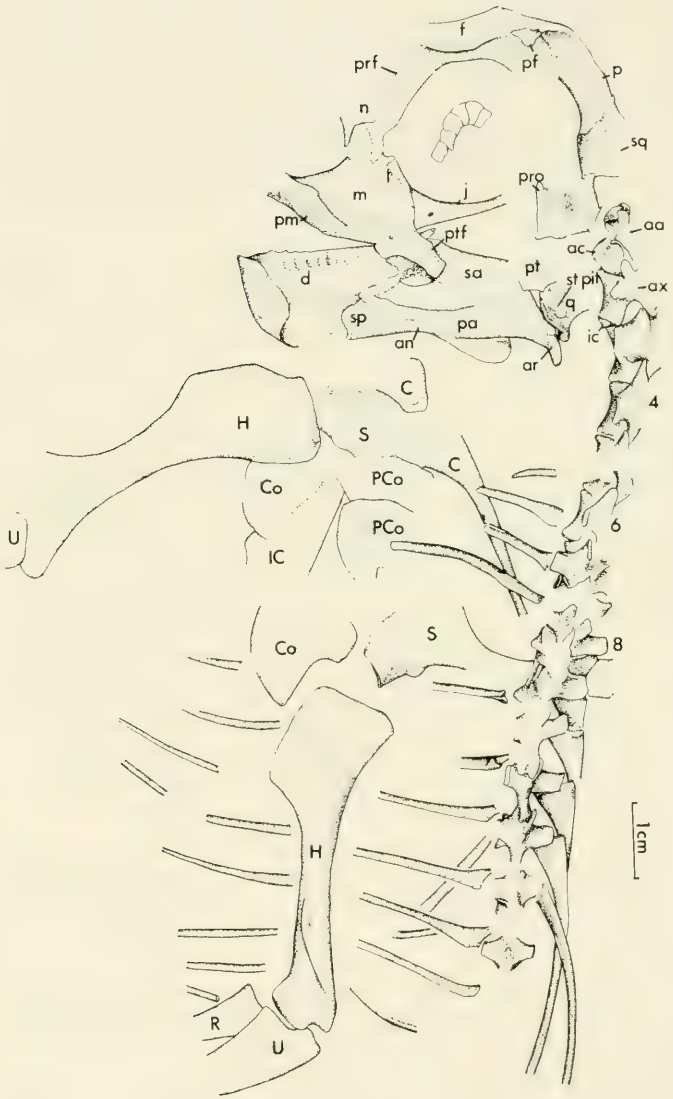
The prefrontal is a triangular bone forming the anterodorsal edge of the orbit. It contacts the lacrimal ventrally, the maxilla and nasal anteriorly, and the frontal dorsally. All of these sutures are squamous interdigitating contacts. The prefrontal is restricted to the lateral surface of the face, the transition from the lateral to dorsal surface occurring at the area of the prefrontal-frontal contact. The lateral surface of the prefrontal is smooth.

The frontals are seen in ventral view. Each frontal contacts the nasal and prefrontal anteriorly, the postfrontal and parietal posteriorly, and its fellow at the midline. No preparietal bone is present,

---

Figure 1. *Galeops whaitsi.* Drawing based on latex peel taken from AMNH-5536.

Abbreviations: an, angular; ar, articular; C, clavicle; Co, coracoid; d, dentary; f, frontal; H, humerus; i, intermedium; IC, interclavicle; j, jugal; l, lacrymal; m, maxilla; n, nasal; p, parietal; pa, prearticular; PCo, procoracoid; pf, postfrontal; pm, premaxilla; po, postorbital; prf, prefrontal; pro, prootic; pt, pterygoid; q, quadrate; qj, quadratojugal; r, radiale; R, radius; S, scapula; sa, surangular; sm, septomaxilla; sq, squamosal; u, ulnare; U, ulna.


f
prf
pf
p
n
sq
f
pro
m
j
pm
aa
ptf
ac
sa
pt
st
pit
ax
d
q
sp
pa
ic
an
ar
C
4
H
S
C
Co
PCo
6
U
PCo
IC
Co
S
8
1cm
H
R
U

so the frontals form the anterior border of the pineal foramen. Laterally, they contribute to the margin of the orbit. Ventrally, strong ridges form the border of the nasal tracts.

The postfrontal is a small, triangular bone wedged between the frontal and postorbital. It has a smooth concave lateral surface.

The postorbital is a tall, narrow bone separating the orbit from the temporal opening. It is supported by the jugal and squamosal ventrally and articulates with the parietal and postfrontal dorsally. It does not extend posteriorly along the parietal to meet the squamosal as is the case in dicynodonts and primitive therapsids generally.

The squamosal is a complex bone that is, in its general structure, like that of dicynodonts. As in dicynodonts, the main body of the bone forms the lateral portion of the occipital plate. The dorsal portion of this area is folded posteriorly so that the posterior rim of the temporal fenestra overhangs the occiput. No such outfolding is seen ventral to the zygomatic bar. A ventrally directed ramus supports the quadrate and quadratojugal and forms the lateral portion of the occipital plate. Laterally, an anteriorly directed zygomatic ramus extends to the jugal. This is a narrow rodlike bone, rather than being flat and beamlike as in dicynodonts. The zygomatic ramus of the squamosal overlaps the jugal, extending well anterior to the posterior edge of the orbit.

The parietals are seen in ventral view (Fig. 4). They have a sutural contact with the frontals and postorbitals anteriorly and with the postparietal posteriorly. Large tabulars are probably present as well, but sutures cannot be clearly identified. Ventrally, each parietal has a crescent-shaped ridge that served as the area of attachment of the epipterygoid and braincase to the skull roof. The

---

Figure 2. *Galeops whaitsi.* Drawing based on latex peel taken from counterpart slab of AMNH 5536. Skull and lower jaw bones are shown from medial surfaces.

Abbreviations: aa, atlas arch; ac, atlas centrum; an, angular; ar, articular; ax, axis; C, clavicle; Co, coracoid; d, dentary; f, frontal; H, humerus; ic, intercentrum; IC, interclavicle; j, jugal; l, lacrymal; m, maxilla; n, nasal; p, parietal; PCo, procoracoid; pf, postfrontal; pm, premaxilla; prf, prefrontal; pro, prootic; q, quadrate; R, radius; S, scapula; sp, splenial; sq, squamosal; st pit, stapedial pit; U, ulna.

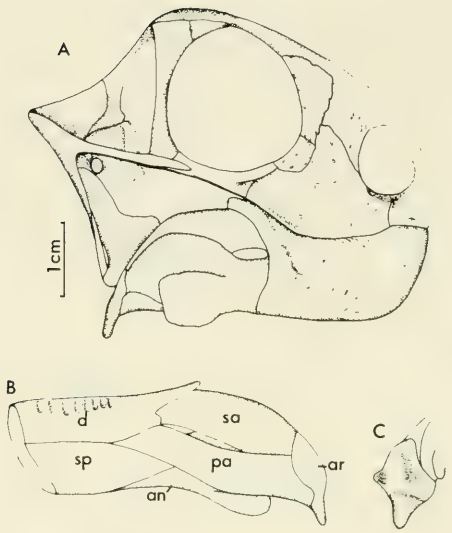


Figure 3. *Galeops whaitsi.* A) reconstruction of skull and lower jaw; B) reconstruction of lower jaw, medial view; C) reconstruction of articular, dorsoposterior view.

Abbreviations: see Figure 2.

parietals extend lateral to this ridge as a ventrally facing shelf that would have provided an area for muscle attachment. This shelf forms a portion of the lateral edge of the temporal fenestra. Anteriorly, a cup-shaped depression is present just anterior and lateral to the area of attachment of the braincase.

The quadratojugal is a small splintlike bone resting on the posterolateral corner of the quadrate ventrally and fitting in a groove on the anterior face of the squamosal dorsally. An oval quadratojugal foramen lies between the quadrate and quadratojugal.

The quadrate is a large bone with a dorsally directed process that fits in a groove in the squamosal, an anteriorly directed flange that

meets the pterygoid, and a ventral expansion that forms the articular surface for the lower jaw. The articular surface is divided into two condyles separated by a deep groove. The lateral condyle is located slightly posterior to the inner condyle. A pit is present on the internal surface of the quadrate that would have received the stapes, although the stapes itself is not preserved.

Braincase: The braincase of *Galeops* is represented by the internal surface of the dorsal half of the occiput (Fig. 4), the lateral surface of the prootic (Fig. 1), and the ventral surface of the basisphenoid (Fig. 5). No sutures can be seen in the occiput. A small posttemporal fenestra is present, surrounded by the squamosal laterally and the occipital plate medially. A groove on the lateral surface of the prootic leads to the temporal fenestra. Two large paired internal carotid foramina are present in the basisphenoid just medial and

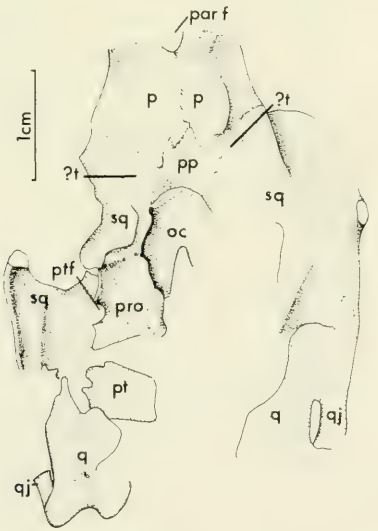


Figure 4. *Galeops whaitsi.* Internal view of posterior surface of skull drawn from latex peel of AMNH 5536.

Abbreviations: oc, occiput; p, parietal; par f, parietal foramen; pp, postparietal; pro, prootic; pt, pterygoid; ptf, posttemporal fenestra; q, quadrate; qj, quadratojugal; sq, squamosal; t, tabular.

posterior to the basipterygoid articulation. Grooves in the basisphenoid lead to these foramina from the posterior edge of the bone. Posterior to the basipterygoid articulation, the lateral edge of the basisphenoid extends ventrally as a large semicircular flange that forms the ventral edge of the fenestra ovalis. This is located well above the level of the stapedial pit on the quadrate, so the stapes would have sloped ventrally, rather than being nearly horizontal as in dicynodonts.

Palate: The palate of *Galeops* (Fig. 5) is primitive in its general structure; a full complement of palatal bones is present, the transverse flange of the pterygoid is present, and the interpterygoidal vacuity is small. An advanced feature is the enlargement of the palatal flanges of the premaxillae to form a secondary palate. The vomers, as in dicynodonts, form vertical plates, although in *Galeops* they are separate ventrally. The palatines have the relationships seen in the primitive anomodont *Otsheria:* each palatine contacts the maxilla and ectopterygoid laterally, the vomers and opposite palatine medially, and the pterygoid posteriorly. The palatines are arched to roof the posterior portion of the internal narial openings. A sharp ridge borders this vaulted area laterally, suggesting that a soft palate was present. The ectopterygoid is a small rectangular bone extending from the transverse flange of the pterygoid to the maxilla. The bone has been displaced slightly, so it is impossible to determine if a lateral palatal foramen was present as in dicynodonts (Cluver, 1975). The pterygoids are partially separated by a small interpterygoid vacuity similar in size and proportions to that of *Otsheria.* The two pterygoids contact one another anterior to this vacuity but do not meet posteriorly, as is the case in dicynodonts, including *Eodicynodon,* the earliest known dicynodont (Barry, 1974). The basipterygoid articulation is unfused. The lateral edge of the transverse flange of the pterygoid is expanded and covered by unfinished bone.

Lower Jaw: The lower jaw of *Galeops* (Figs. 1–3) is short and deep with a vertical unfused symphysis and a straight ventral edge. A fenestra is present on the lateral surface of the jaw between the dentary, surangular, and angular. A distinct coronoid process is not present, although the posterior edge of the dentary extends above

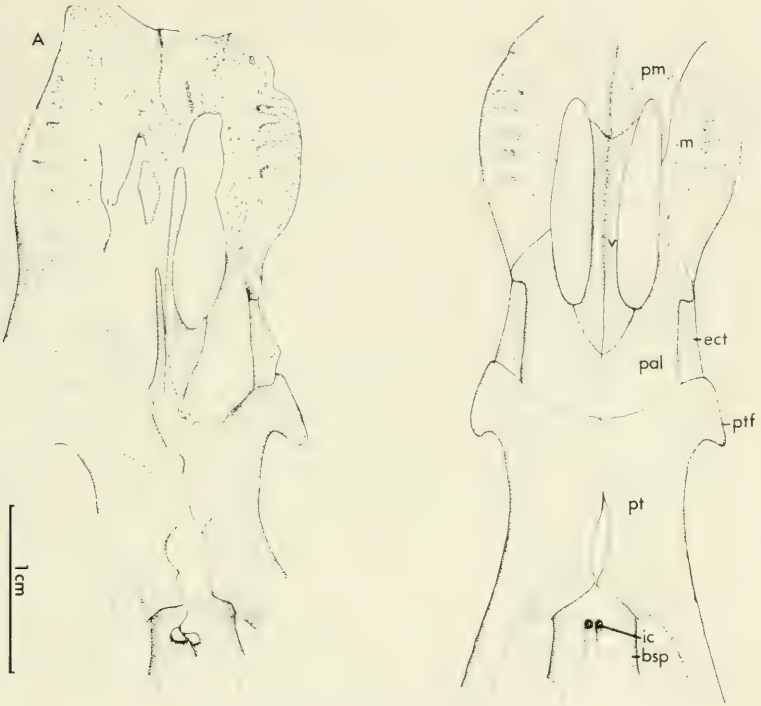


Figure 5. The palate of *Galeops whaitsi.* A) as preserved in AMNH 5536; B) reconstruction.

Abbreviations: bsp, basisphenoid; ect, ectopterygoid; ic, foramen for internal carotid artery; m, maxilla; pal, palatine; pm, premaxilla; pt, pterygoid; ptf, transverse flange of pterygoid; v, vomer.

the level of the postdentary bones. A small ventrally directed retroarticular process is present.

The dentary forms the anterior half of the lower jaw. Except for a small posterior area, the lateral surface of the dentary is covered by numerous small pits and grooves. Posteriorly, the surface is smooth and is depressed below the anterior portion of the bone. This arrangement, which is similar to that of dicynodonts, suggests that the muscles extended onto the posterior portion of the dentary and that a horny beak was present anteriorly. In contrast to most dicynodonts, no longitudinal groove is present on the upper edge of the dentary lateral to the tooth row.

Internally, only the upper half of the dentary is exposed, the ventral half being covered by the splenial. The anterior end of the dentary is without teeth; posterior to this, eight sockets are present for teeth along the lateral margin of the bone. The anterior sockets are slightly larger than the posterior sockets, indicating that tooth size increased anteriorly. There is no indication that a distinct canine was present. All of the sockets are vertical. The tooth row of the dentary is longer than the tooth row of the maxilla, suggesting that some anteroposterior movement of the jaw occurred during closing.

The splenial is restricted to the internal surface of the lower jaw. Posteriorly, the splenial is wedged between the angular and prearticular. It is incompletely preserved anteriorly, although grooves in the dentary show that it extended to the symphysis.

The angular forms most of the lateral surface of the posterior half of the jaw. Its most prominent feature is the reflected lamina, which separates from the angular at the posterior edge of the lateral mandibular fenestra and extends posteriorly and ventrally as a thin sheath of bone.

The prearticular is a broad crescent-shaped bone that extends from the articular to the dentary. It forms the ventral edge of the lower jaw posteriorly, but its lateral exposure is reduced anteriorly so that at the posterior edge of the reflected lamina it is restricted to the internal surface of the jaw. The prearticular most probably formed the margin of the adductor fossa, but since the dorsal portion of the bone is not preserved, the full extent of the fossa is unknown.

The surangular extends from the dentary to the articular, forming the dorsal margin of the postdentary region of the jaw. It is extensively overlapped by the angular so that, in lateral view, it is restricted to the dorsal margin of the jaw, but in medial view, it extends halfway down the internal surface of the jaw.

The articular is supported by the prearticular, angular, and surangular. It forms both the articular surface for the quadrate and the retroarticular process. The articular surface faces strongly posteriorly. It is differentiated into two grooves separated by a rounded ridge. The lateral groove is elongate anteroposteriorly, strongly concave mediolaterally and slightly so anteroposteriorly. A small medially directed shelf forms the medial groove.

The internal surface of the postdentary region is partially covered

by the transverse flange of the pterygoid, so the presence of a coronoid is uncertain.

Vertebrae: The first fourteen vertebrae of *Galeops* are present (Figs. 6, 7), although many of these are incompletely preserved. Cox (1959) differentiated the cervical from the trunk vertebrae of the dicynodont *Kingoria* on the basis of the size of the parapophysis and diapophysis and the thickness of the associated ribs, the cervical vertebrae having more poorly developed parapophyses and more slender ribs. In *Galeops,* a well-developed parapophysis is first seen in the seventh vertebra. No parapophysis can be seen on the corresponding area of the sixth vertebra, although a small one may have been present ventrally. Thus, the first six vertebrae can be considered to be cervicals.

The atlas-axis complex is well-preserved (Fig. 6). It is primitive in its general construction: the atlas centrum and axis are separate, and judging from the articular surfaces, separate atlas and axis intercentra and proatlases would have been present. The atlas arches

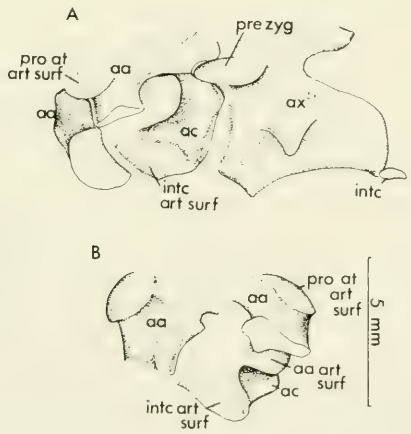


Figure 6. The atlas-axis complex of *Galeops whaitsi.* A) lateral view; B) anterior view of atlas arch and centrum. Drawing based on latex peels from AMNH 5536.

Abbreviations: aa, atlas arch; aa art surf, articular surface for atlas arch; ac, atlas centrum; ax, axis; intc, intercentrum; intc art surf, articular surface for intercentrum; prezyg, prezygopophysis; pro at art surf, articular surface for proatlas.

meet above the neural canal. Transverse processes are present on these elements sloping posteriorly and ventrally. The atlas centrum does not extend to the ventral edge of the vertebral column. It has a trefoil-shaped articular surface anteriorly. The neural spine of the axis is not preserved. The prezygapophysis is convex and faces dorsolaterally. A well-developed transverse process is present on the axis extending posteriorly and ventrally from the base of the neural arch.

Both the cervical and dorsal vertebrae are deeply amphicoelous. A sharp ventral keel is present on the centra. The neural arches are not fused to the centrum, although the sutural attachment is intimate. The base of the neural arch is located anteriorly on the centrum. A large intercentrum is present between the sixth and seventh vertebrae, and presumably intercentra would have been present between the more anterior vertebrae. A small intercentrum is located between the seventh and eighth vertebrae. None is present posterior to this.

A number of structural changes can be seen posteriorly along the vertebral column:

1) The transverse process moves dorsally. The transverse process of the axis is located at the dorsal margin of the centrum. On the fourth vertebra, it is located more dorsally on the lateral surface of the neural arch. The position of the process of the following three vertebrae is similar. A further dorsal migration is seen between the seventh and ninth vertebrae, with the transverse process reaching the level of the zygapophysis.

2) The inclination of the transverse process changes from ventral to dorsal. On the axis, the transverse process slopes ventrally and posteriorly. On the fourth vertebra, the process is nearly horizontal and is directed laterally. On the eighth vertebra, a distinct dorsal inclination is seen. This is further accentuated on the more posterior vertebrae.

3) The parapophyses move dorsally. A distinct parapophysis is first seen on the seventh vertebra, where it is located well down on the anterior edge of the centrum. The intercentrum and posterior edge of the sixth vertebra also contribute to its formation. The parapophysis of the eighth vertebra is located slightly higher, and the articular surface does not extend onto the seventh vertebra. The parapophysis of the eleventh vertebra is located about midway

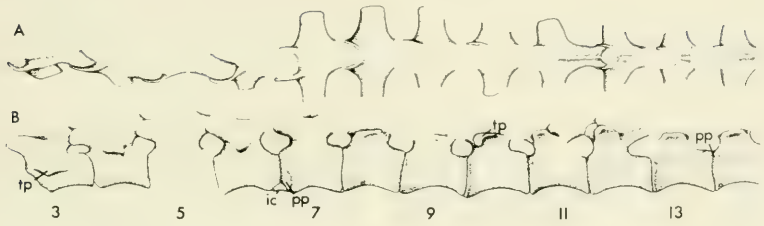


Figure 7. The vertebral column posterior to the axis of *Galeops whaitsi* in A) dorsal and B) lateral views. Based on latex peels taken from AMNH 5536.

Abbreviations: ic, intercentrum; pp, parapophysis; tp, transverse process.

between the dorsal and ventral edges of the centrum. On the fourteenth vertebra, the parapophysis is located on the dorsal margin of the centrum close to the transverse process, although the capitular and tubercular articular surfaces of the rib head remain distinct. There is no indication that the diapophysis migrates ventrally from the transverse process, as in dicynodonts (Cox, 1959).

4) The zygapophyses move closer to the midline. On the sixth vertebra, the first vertebra on which the zygapophyses are clearly preserved, the zygapophyses are located at the edge of the centrum and are inclined about 45° to the horizontal. The seventh to eleventh vertebrae show a medial movement of the zygapophyses and an increase in the angle that they make with the horizontal from about 45° to about 60°. The medial movement of the postzygapophyses results in a coalescence of the processes supporting the articular surfaces, resulting in a single posteriorly directed process.

Ribs: Of the cervical ribs of *Galeops,* only those associated with the fifth and sixth vertebrae are preserved (Figs. 1, 2). Although both of these are incomplete, they are distinctly less robust than the more posterior ribs.

The first nine thoracic ribs are at least partially preserved. All of these are double-headed. The tuberculum terminates the shaft of the rib, and the capitular articular surface is formed by a process that extends ventrally at an angle of about 35° to the shaft. The thoracic ribs are only slightly curved. In the right rib associated with the

twelfth vertebra, the shaft of the rib extends nearly straight from the tubercular surface for about a quarter of the length of the rib. Thus *Galeops* probably had a tall laterally compressed body.

Pectoral Girdle: The pectoral girdle of *Galeops* is formed by the paired clavicles, coracoids, procoracoids, and scapulae and by a single median interclavicle (Figs. 1, 2). There is no evidence that either a cleithrum or an ossified sternum was present.

The scapula has a tall, slender blade and an expanded platelike base. A prominent tubercle for the scapular head of the triceps is present on the posterior edge of the bone just proximal to the glenoid. A distinct acromion process is not present, nor is a scapular spine developed as is the case in dicynodonts (Boonstra, 1966).

The coracoid and procoracoid are subequal in size. The glenoid is formed by the scapula and coracoid. The primitive screw-shaped structure of the glenoid has been lost; the glenoid of *Galeops* is short and faces posterolaterally. The coracoid extends posterior to the glenoid. The coracoid foramen is located within the procoracoid.

The clavicle has a triangular base and a rodlike stem. The interclavicle is a long paddle-shaped element. Its head is not preserved. Distinct grooves for a sternum are not present in the stem.

Humerus: The humerus of *Galeops* is a slender bone with moderately expanded proximal and distal ends in a distinct shaft (Fig. 8). The proximal and distal ends are distinctly, but not strongly, twisted on one another; when viewed proximally, the angle between the long axes of the two ends is about 40°. The proximal end of the humerus curves strongly dorsally; when seen in anterodorsal view (Fig. 8B), the dorsal third of the humerus makes an angle of about 120° with the distal third of the humerus. The entepicondyle is well developed, and an entepicondylar foramen is present. The ectepicondyle is poorly developed, and no ectepicondylar foramen is present. A groove passing proximodistally along the lateral edge of the bone presumably held the nerves and vessels that usually pass through the ectepicondylar foramen. The ulnar articular surface is distinct and well developed. It faces primarily ventrally, although it extends onto the distal end of the humerus. The radial condyle, although distinct, is not a strongly rounded capitulum like that seen in gorgonopsians and dicynodonts (Boonstra, 1965, 1966).

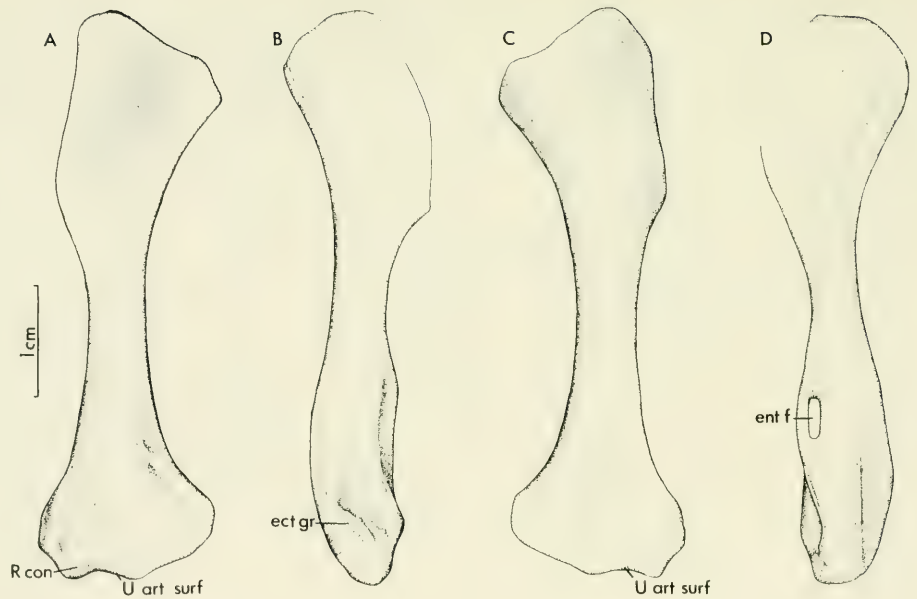


Figure 8. The humerus of *Galeops whaitsi* in A) anteroventral; B) anterodorsal; C) posterodorsal; and D) posteroventral views. Based on AMNH 5536.

Abbreviations: ect gr, ectepicondylar groove; ent f, entepicondylar foramen; R con, radial condyle; U art surf, articular surface for ulna.

Radius: The radius of *Galeops* is a slender bone about 60 percent of the length of the humerus. The proximal articular surface is oval in outline and is slightly concave. The distal articular surface is also oval.

Ulna: The ulna of *Galeops* is slightly longer than the radius (Figs. 1, 2). The olecranon process is prominent, extending well past the humeral articular surface. The humeral articular surface is a well-defined notch. Lateral to this, a distinct articular surface for the radius is present.

Carpus: Only the dorsal surface of the proximal carpal bones of *Galeops* is seen (Fig. 1). The radiale is short and has a small area of finished bone on its dorsal surface. The intermedium and ulnare are elongate. They have a large area of contact with one another proximal to the perforating foramen. A portion of the lateral centrale is present. This supports the intermedium and forms the distolateral corner of the perforating foramen.

GALEPUS

Materials and Methods: Galepus is represented by a single species, *Galepus jouberti,* and by a single specimen, AMNH 5541, that comes from the *Cistecephalus* zone of the Beaufort series of South Africa. Much of the skull and skeleton is represented by impressions in a coarse sandstone from which latex peels were made. Unfortunately, the counterpart block was not preserved, so it was not possible to cast individual elements in three dimensions.

Skull: The skull of *Galepus* is represented by a cast of the internal surface of the roofing bones and of the palatal flanges of the premaxillae (Figs. 9, 12). It is similar to that of *Galeops* in its general structure: the orbits and external narial openings are large; the face and postorbital region of the skull are short; a large oval pineal opening is present; the ventral margin of the postorbital region of the skull is deeply emarginated; the occiput slopes forwards; the orbit is bounded posteriorly by a tall narrow postorbital; a secondary palate formed by the palatal flanges of the premaxillae is present; and the internal surface of the parietal is marked by a crescentic ridge and a cup-shaped depression antero-

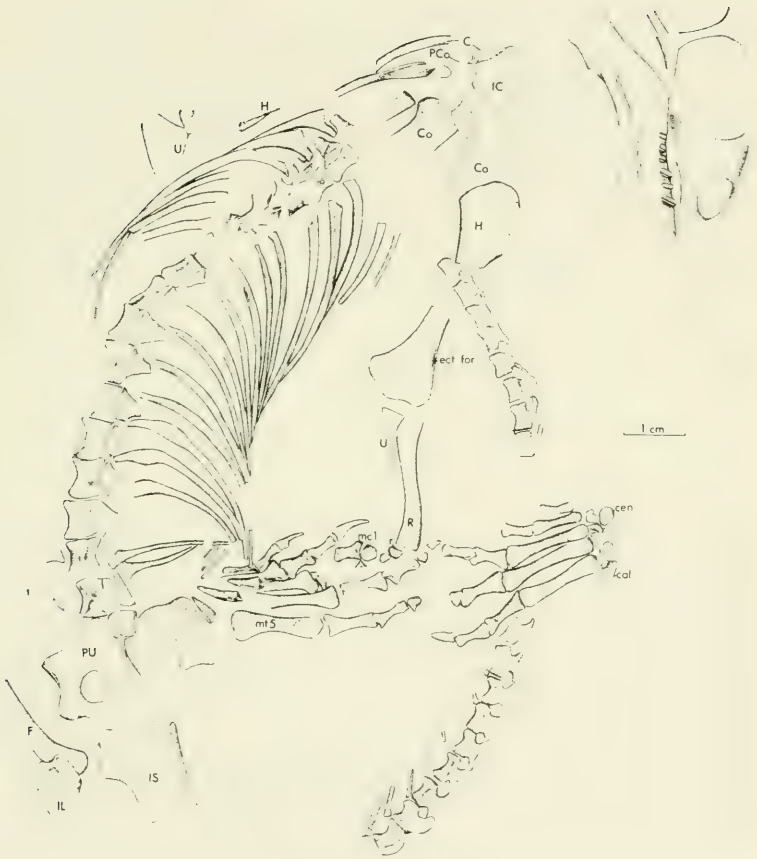


Figure 9. *Galepus jouberti.* Drawing based on latex peel taken from AMNH 5541. Skull and lower jaw bones viewed from medial surface.

Abbreviations: C, clavicle; cal, calcaneum; cen, centrale; Co, coracoid; ect for, ectepicondylar foramen; F, femur; H, humerus; IC, interclavicle; IL, ilium; IS, ischium; mc 1, first metacarpal; mt 5, fifth metatarsal; PCo, procoracoid; PU, pubis; r, radiale; R, radius; U, ulna.

lateral to this ridge. Unfortunately the sutures referred to by Broom (1914) have been obliterated, so the exact relationships of the individual skull elements are uncertain.

The left lower jaw is visible in internal view. It is more slender than the jaw of *Galeops,* and its outline differs: the ventral margin of the jaw, rather than being straight as in *Galeops,* is slightly concave in profile, and the dorsal margin of the postdentary region extends nearly straight from the dentary to the articular, rather than being gently convex as in *Galeops.* A splenial is not preserved, but grooves in the dentary indicate that it extended to the symphysis. The sutures between the postdentary bones cannot be identified.

Six small peglike teeth are preserved in the dentary and an empty aveolus is present anterior to these. A small edentulous region is present anterior to the tooth row. Unlike *Galeops* where the sockets, and presumably the teeth they contained, are vertical, the teeth of *Galepus* slope anteriorly.

Postcranial Skeleton: A series of eighteen dorsal vertebrae of *Galepus* is present. These are deeply amphicoelous and show a sutural attachment between the neural arch and centrum. The structure of the neural arch is seen clearly only in the fifth vertebra from the anterior end of the preserved series. It is like the neural arch of the corresponding vertebra in *Galeops:* the zygapophyses are strongly tilted and are near the midline, the postzygapophyses are coalesced so the articular surfaces appear to be formed by a single posteriorly directed process, and the transverse processes are large dorsolaterally directed structures located at the level of the zygapophyses.

The caudal region is represented by two disconnected series of vertebrae, an anterior series of nine vertebrae and a posterior series of eight vertebrae. They are separated by a space that would have been occupied by six vertebrae and are separated from the sacral region by a space that would have been occupied by about eight vertebrae. Thus the tail would have included at least 31 vertebrae. These decrease in both height and length posteriorly. The zygapophyses slope less steeply than in the dorsal series. A prominent transverse process is located at the base of the neural arch on the first vertebra in the series. No transverse process is seen on any of the more posterior vertebrae. Haemal spines and arches are present

between all the vertebrae in the proximal series and between the first two vertebrae in the posterior series.

Eighteen ribs are at least partially preserved on the right and six on the left side. In all the ribs, the curvature is greatest near the head, with the distal half of the rib being nearly straight and at an angle of 30° to the proximal portion. The heads of the first three ribs on the left side and the last two ribs on the right side are visible. The anterior ribs are double-headed. The posterior ribs are single-headed.

The pectoral girdle is seen in internal view. A large interclavicle is present with a paddle-shaped stem and a diamond-shaped head. No ossified sternum is present. The clavicle has a long narrow riblike stem and a triangular head. The coracoids, procoracoids, and scapulae are too poorly preserved for their structure to be fully determined.

The humerus of *Galepus* is like that of *Galeops* in its proportions and general features. In both, the entepicondyle is well developed, the ectepicondyle is reduced, the proximal and distal ends are distinctly twisted on one another, the ulnar surface faces strongly ventral but also extends onto the distal surface of the bone, and the pectoral crest is restricted to the proximal third of the bone. The humerus of *Galepus* differs from that of *Galeops* in having an ectepicondylar foramen and in the lack of an upturning of the proximal end, the dorsal edge being nearly straight in anterodorsal view.

Only the medial surface of the proximal end of the ulna is preserved. As in *Galeops* an olecranon process is present, and the medial surface of the proximal end of the ulna is concave. The right radius is seen in lateral aspect. It is like the radius of *Galeops* in its proportions and in having a slight S-shaped curve.

The hand overlies the foot, although much of the hand is missing, exposing the metatarsals and phalanges of the foot.

Only three elements of the carpus are present, these being the radiale, lateral centrale and first distal carpal. The radiale is short and without finished bone. The first distal carpal is subcircular and has a large area of finished bone on its ventral surface.

Of the metacarpus, only the first metacarpal is present. This is a short phalangelike element. A large tubercle is present on the lateral edge of the bone near its proximal end. The toes are represented by three long, clawlike terminal phalanges.

The pelvis is seen in internal view. It is primitive in having a large pubis and ischium and in having well-developed anterior and posterior extensions of the iliac blade. An advanced feature is the enlargement of the obturator foramen.

The dorsal surface of the proximal end of the left femur is visible. The proximal end of the femur is tilted dorsally about 35° from the shaft of the bone.

The tarsus is represented by an incompletely preserved right calcaneum, centrale, and the first four distal tarsals, all visible in ventral view. The calcaneum is a tall, platelike element with a notch for the perforating foramen on its medial edge. The centrale is a cubical cartilage-covered element. The first three distal tarsals are subequal in size. The fourth is larger, although it is less than twice the size of the third in its linear dimensions.

All five metatarsals are present, visible in ventral view. They increase in size from the first to the fourth with the fifth being about equal to the third in length. The phalangeal formula of the pes is 2,3,?,?,3. The terminal phalanges, where known, are elongate, clawlike elements.

GALECHIRUS

Materials and Methods: Galechirus is represented by a single species, *Galechirus scholtzi,* and by two specimens: SAM 1068, which shows the front half of the skull and the lower jaw in lateral view and much of the postcranial skeleton (Fig. 10); and AMNH 5516 (now housed in the South African Museum), which shows a pelvic and pectoral limb and fragmentary ribs and vertebrae (Fig. 11). Both of these specimens come from the *Cistecephalus* zone of the Beaufort series of South Africa (Kitching, 1977). They are preserved as natural casts. Molds taken from these specimens provided a positive image that served as the basis for the descriptions and drawings.

Skull: The skull of *Galechirus* (Fig. 10) is like that of *Galeops* in having large orbits and external narial openings, a short temporal region, and a deep emargination of the cheek posterior to the orbit. In contrast to the condition in *Galeops, Galechirus* retains premaxillary teeth and has a more elongate face.

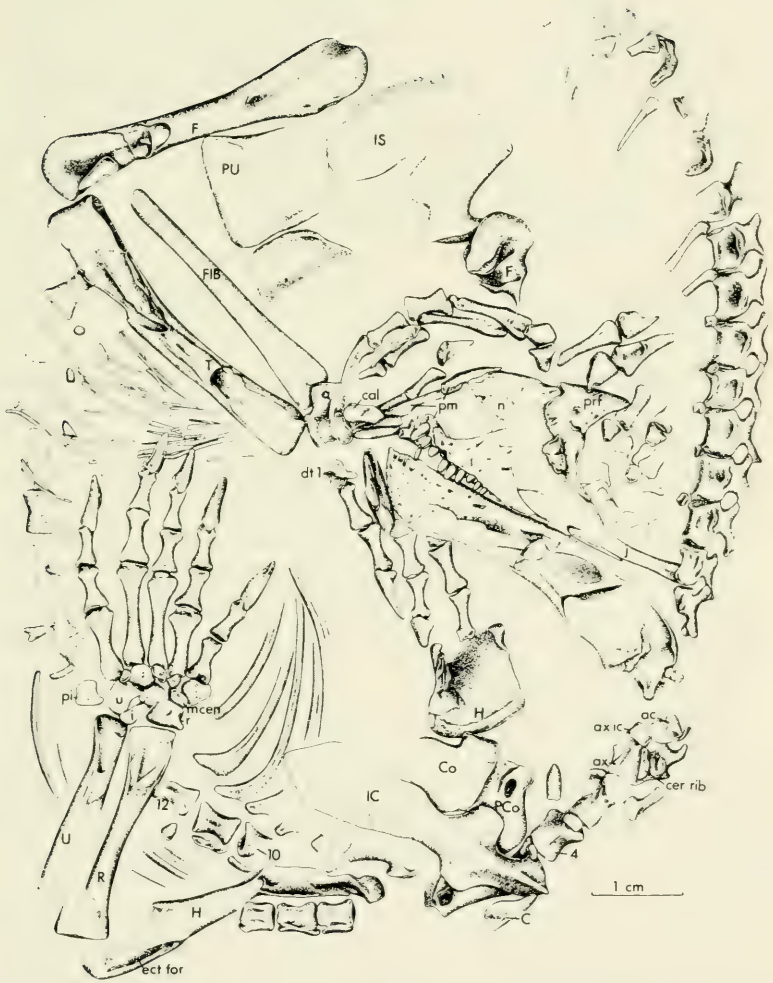


Figure 10. *Galechirus scholtzi.* Drawing based on latex peel taken from SAM 1068.

Abbreviations: a, astragalus; ac, atlas centrum; ax, axis; ax ic, axis intercentrum; C, clavicle; cal, calcaneum; cer rib, cervicle rib; dt 1, first distal tarsal; ect for, ectepicondylar foramen; F, femur; FIB, fibula; H, humerus, i, intermedium; IS ischium; j, jugal; m cen, medial centrale; pi, pisiform; pm, premaxilla; prf, prefrontal; PU, pubis; T, tibia; u, ulnare; U, ulna.

The arrangement of the bones of the face in *Galechirus* is similar to that of *Galeops*. The premaxilla-maxilla contact is located midway below the external narial opening. A separate bone, presumably the septomaxilla, is present internal to the premaxilla-maxilla contact. The maxilla meets the nasals midway along the posterior edge of the external narial opening. The maxilla-nasal suture slopes dorsoposteriorly from this point. Unfortunately, the sutures between the maxilla and more posterior bones are obscure, so the relationship of these bones is uncertain. Six small peglike teeth are present in the maxilla, and an empty socket is present posterior to these. The anterior three teeth are subequal in size and are slightly larger than the posterior three teeth.

The premaxillae are separate. Each premaxilla has a well-developed dorsal ramus that extends between the nasals and a ventral ramus that meets the maxilla midway below the external narial opening. The right premaxilla, which is seen in internal view, contains two large, procumbent, chisel-shaped teeth. Three teeth are present in the preserved portion of the left premaxilla. The posterior two are approximately equal to the maxillary teeth in size and are vertically oriented. The more anterior tooth is slightly larger and slopes anteriorly. The missing portion of the premaxilla probably held two large procumbent teeth similar to those seen in the right premaxilla.

The prefrontal, which has been displaced slightly, is a triangular element forming the anterodorsal margin of the orbit. Its lateral surface is smooth and curves onto the dorsal surface of the skull.

The suborbital portion of the jugal is a narrow rodlike bone. Posteriorly, a groove is present on its lateral surface, probably for an overlying zygomatic branch of the squamosal.

Lower Jaw: The lower jaw of *Galechirus* is long and slender. Its ventral edge curves upwards, and the symphysis slopes forward. The dentary forms the anterior two-thirds of the jaw. Its lateral surface is covered by numerous small pits and grooves anteriorly. Posteriorly, the surface is smooth and is recessed below the more anterior portion of the dentary. Presumably the adductor muscles inserted on this area of the dentary. Only one tooth is preserved in the dentary. This is a small peglike element located well anteriorly. There does not appear to be room anterior to this for large

procumbent teeth similar to those seen in the premaxilla, nor is there any evidence that such teeth were present.

The dorsal edge of the postdentary region of the jaw curves evenly from the posterior edge of the dentary to the articular. A fenestra is present between the dentary and the postdentary bones. The reflected lamina of the angular separates from the angular at the posterior edge of the fenestra. A small ventrally directed retroarticular process is present beneath the jaw joint. The sutures between the individual bones of the postdentary region of the jaw are not visible.

Postcranial Skeleton: The vertebral column of *Galechirus* is partially preserved in SAM 1068. Anteriorly, four cervical vertebrae are present between the posterior end of the jaw and the pectoral girdle. The first vertebra in this series is the atlas, the centrum of which is seen in lateral view. As in *Galeops,* it does not reach the ventral surface of the vertebral column. A large axis intercentrum is present as a distinct element between the atlas centrum and the axis. The following vertebrae are short and broad, their length being about equal to their width across the posterior end of the centrum. The axis has a posteroventrally directed transverse process located well down on the neural arch. The centrum does not have a sharp ventral keel, although a low ridge is present. The following two vertebrae are seen in ventral view. A distinct ventral keel is present, and intercentra are present between each of these vertebrae.

A series of three dorsal vertebrae, probably the tenth to twelfth, lies between the shoulder girdle and the hand. These are seen in ventral view. The keel has been reduced and intercentra are absent. Distinct articular surfaces for the heads of the ribs are not visible.

Faint traces of eight presacral vertebrae are present between the wrist and the knee. Little of their structure can be determined.

The caudal vertebrae are represented by two series: an anterior series of twelve vertebrae and a more posterior series of three vertebrae. A space equal in length to four centra is present between the anterior series and the pelvis, and the two sections of the tail are separated by a space equal in length to about ten centra. Thus, the tail would have had in excess of 29 vertebrae.

The caudal vertebrae decrease both in height and length posteriorly. Haemal arches are present between each of the first ten vertebrae, and transverse processes are present on each of the

vertebrae in the anterior series. The more posterior vertebrae have neither transverse processes nor haemal arches.

Three ribs are preserved in SAM 1068. These are associated with the three vertebrae seen between the shoulder girdle and the hand. The more anterior of these is clearly double-headed. The separation of the two articular surfaces is less distinct posteriorly.

Small, needle-like gastralia are present posteriorly, but these are disturbed so their natural arrangement is unknown. This is the only evidence of gastralia in therapsids (Romer, 1956).

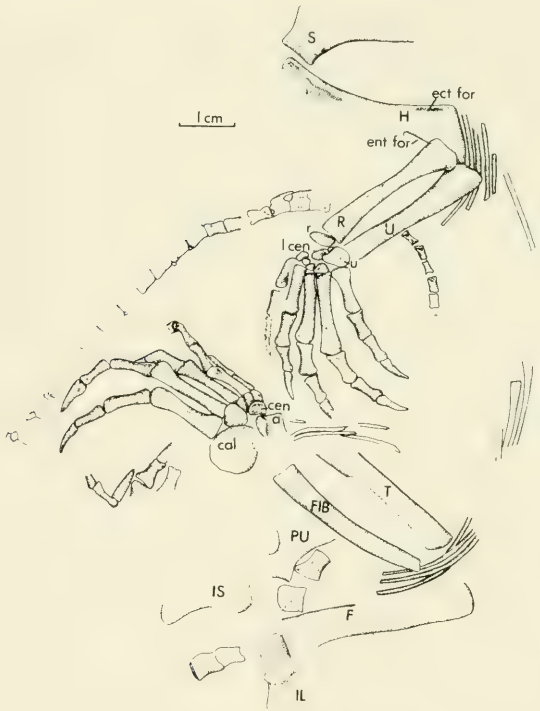


Figure 11. *Galechirus scholtzi.* Drawing based on cast of AMNH 5516 (now housed in the South African Museum).

Abbreviations: a, astragalus; cal, calcaneum; cen, centrale; ect for, ectepicondylar foramen; ent for, entepicondylar foramen; F, femur; FIB, fibula; IL, ilium; IS, ischium; l cen, lateral centrale; PU, pubis; r, radiale; R, radius; S, scapula; T, tibia; u, ulnare; U, ulna.

The pectoral girdle is seen in ventral view in SAM 1068 and in lateral view in AMNH 5516. The scapulae have tall, slender blades and expanded platelike bases. A distinct rugosity on the posterior edge of the scapular blade just proximal to the glenoid marks the site of the origin of the scapular head of the triceps. An acromion process is not present.

The coracoid and procoracoid are both large, with the coracoid extending well posterior to the glenoid. The procoracoid foramen is located within the procoracoid just proximal to the glenoid. The interclavicle has a diamond-shaped head and a broad paddle-shaped stem. The head of the interclavicle is recessed ventrally to receive the medial end of the clavicle.

The left humerus is seen in ventral view in both specimens. The proportions of this element are similar to the proportions of the humerus of *Galeops:* it is a slender bone with a well-defined shaft and with little expansion of the proximal and distal ends. The pectoral crest is restricted to the proximal third of the bone. In contrast to the condition in *Galeops,* both an ectepicondylar and ectepicondylar foramen are present.

The radius is a slender bone, slightly shorter than the humerus. It has a slight S-shaped curvature. The ulna is almost identical to that of *Galeops* in its proportions and in the development of the articular surfaces, although the olecranon process is less well developed. This difference may be a result of differences in the ontogenetic stage of development of the specimens.

A complete carpus is present in SAM 1068 and most of the carpus is present in AMNH 5516. All the elements primitively present in the synapsid carpus are present, although these are all shortened proximodistally so the length of the carpus is less than that of the metacarpus. A distinctive feature is the expansion of the ulnare to form a flat platelike bone.

The metacarpals increase in length from the first to the fourth, with the fifth being about equal to the second in length. The phalangeal formula is 2,3,3,3,3. The terminal phalanges are elongate, laterally compressed, clawlike elements.

The pelvis is seen in ventral view in SAM 1068 and in lateral view in AMNH 5516. The pubis and ischium are large, platelike elements. The pubis is damaged, so the size of the obturator foramen is uncertain. The ilium is not completely known, although the pre-

served portion shows that it had a tall, slender blade that extends posterior to the acetabulum.

The femur is seen in postaxial view in both specimens. It is equal in length to the humerus. The head of the femur is incompletely preserved, although there is no indication of a dorsal tilting of the proximal end such as is seen in *Galepus*. Also, no downturning of the distal end of the femur is seen.

The tibia and fibula are elongate, slender bones approximately equal in length to the femur and substantially longer than the radius and ulna. Both bones are slightly curved with the concave edges of the bones facing one another. The tibia is more robust than the fibula, the diameter of the tibia at its narrowest point being about twice the minimum diameter of the fibula.

A nearly complete tarsus is seen in dorsal view in AMNH 5516, and an astragalus is seen in dorsal view in SAM 1068. The calcaneum is a large platelike bone. The astragalus is L-shaped. A perforating foramen passes between the astragalus and calcaneum. Distal to the perforating foramen, the articular surface on the astragalus for the calcaneum is strongly convex and extends onto the dorsal surface of the bone. Proximal to the perforating foramen, the articular surface on the astragalus for the calcaneum is concave. The tibial articular surface is restricted to the medial edge of the astragalus. The centrale is a small, cartilage-covered bone located between the astragalus and first four distal tarsals. The distal tarsal row consists of four elements, the fifth distal tarsal having been lost. The first three are subequal in size, the fourth is about three times the size of the third in its linear dimensions.

The metatarsals increase in length from the first to the fourth, with the fifth being about equal to the third in length. The phalangeal formula is 2,3,3,3,3. The terminal phalanges are elongate, laterally compressed clawlike elements.

DISCUSSION

In considering the general evolution of therapsids, Hopson (1969) recognized three basic groups: the Dinocephalia, characterized by an interlocking of the incisors and the presence of a jaw joint that permits no anteroposterior movement of the jaw; the Theriodontia, characterized by the development of a movable quadrate permitting some anteroposterior movement of the lower jaw; and the Anomo-

dontia, characterized by the ventral emargination of the cheek posterior to the orbit and a jaw joint that permits considerable anteroposterior movement of the lower jaw on the fixed quadrate. The emargination of the cheek in the dromasaurs immediately indicates that they belong within the Anomodontia. This placement is supported by features of the skull of dromasaurs that are similar to other anomodonts, including: 1) the formation of a secondary palate by palatal flanges of the premaxillae and 2) the presence of a lateral mandibular fenestra.

The most primitive anomodonts known are the venjukoviamorphs *Otsheria* and *Venjukovia* from the Middle Permian of Russia. These show the diagnostic feature of an emarginated cheek, but, relative to dicynodonts, retain a primitive jaw joint, a primitive palate, and primitive features in the temporal region (Watson, 1948; Olson, 1962; Barghusen, 1976). In many respects, the dromasaurs are at the same grade of evolution as are the venjukoviamorphs. This is demonstrated by the following features, which are shared by dromasaurs and the venjukoviamorphs and which are different from the more derived condition seen in dicynodonts:

1) No outfolding of the squamosal is present ventral to the zygomatic ramus of the squamosal. In dicynodonts, such an outfolding is present.
2) The palate is more primitive in showing a small interpterygoid vacuity, transverse flanges on the pterygoids, an unfused basipterygoid joint, and a smaller secondary palate. In dicynodonts, the interpterygoid vacuity has enlarged so that it extends forward between the posterior ends of the vomers, the transverse flanges of the pterygoids have been lost, and the pterygoids are sutured to one another posterior to the interpterygoid vacuity (Cluver, 1970).
3) The articular, as in *Venjukovia* (Watson, 1948), retains a central ridge with two concave depressions on either side of it. In dicynodonts, the central ridge is convex in profile, and a concave area is present anterior to this (Crompton and Hotton, 1967).

In addition, a number of features seen in the dromasaurs, but not known at present in the venjukoviamorphs, are more primitive than the condition in dicynodonts. These include:

1) A separate atlas centrum and axis intercentrum are present in the dromasaurs. In dicynodonts, these fuse to the axis (Cox, 1959). However, the atlas centrum and axis may fuse during ontogenetic development in the dromasaurs.
2) No scapular spine or acromion process is present on the scapulocoracoid. In dicynodonts, both these features are present (Boonstra, 1966).
3) The shape of the interclavicle and the absence of a sternum in the dromasaurs is primitive. In dicynodonts, the interclavicle is short and a large sternum is present (Boonstra, 1966).
4) The iliac blade in the dromasaurs is primitive in having a well-developed posterior process. In dicynodonts, the anterior ramus of the ilium is more strongly developed than the posterior ramus (Boonstra, 1966).

Despite the primitive structure of the dromasaurs, features are present that are advanced over the condition seen in the venjukoviamorphs and are similar to the condition seen in dicynodonts. One of these is the structure of the jugal. In *Otsheria,* the jugal is a triradiate bone retaining well-developed zygomatic and postorbital branches. In *Venjukovia,* the postorbital branch has been reduced although it is still present (Barghusen, 1976). In both dromasaurs and dicynodonts, the postorbital and zygomatic branches of the jugal have been reduced or lost. A second advanced feature is the presence of a smooth area on the posterior end of the dentary that suggests that the adductor muscles extended onto the lateral surface of the dentary. In *Venjukovia,* an external mandibular muscle was present, although it had only a small area of insertion on the lateral surface of the dentary (Barghusen, 1976). A third advanced feature is the structure of the septomaxilla. In *Otsheria* and *Venjukovia,* as in primitive therapsids generally, the septomaxilla is a large element with an exposure on the lateral surface of the face. In dicynodonts and dromasaurs, the septomaxilla is reduced; in the dromasaurs, it is restricted to the floor of the external narial opening.

This combination of primitive and derived features demonstrates that the dromasaurs are members of a grade of evolution intermediate between the venjukoviamorphs and the dicynodonts, but it does not demonstrate that it is a monophyletic group. For this, it is necessary to show that features are present in the three genera that are advanced over the primitive anomodont condition but are not

shared with dicynodonts. The most obvious such feature is the dentition, which consists of reduced peglike teeth. This is a clear difference from both the primitive anomodont condition and the dicynodont condition in which distinct canines are present. An additional derived feature that separates dromasaurs from dicynodonts is the presence of a tall, narrow postorbital and a slender, rodlike lower temporal bar. In dicynodonts, the postorbital bar is low and the lower temporal bar is a flat, beamlike element.

Also the absence of a contact between the postorbital and squamosal is a derived feature different from the condition in both dicynodonts and venjukoviamorphs, where the postorbital extends along the upper margin of the temporal opening to reach the squamosal. However, the only dromasaur in which the posterior extent of the postorbital is known is *Galeops,* so the possibility that this is a derived feature present only in that genus cannot be discounted.

Thus the present evidence, although not conclusive, suggests that the dromasaurs are a natural group. Within the group, the three genera can be placed in a single structural sequence with *Galechirus* being the most primitive and *Galeops* being the most derived member of the sequence. The features that document this series are:

1) *The Tooth Row:* In *Galechirus,* premaxillary teeth are present; in *Galepus,* premaxillary teeth are absent but the edentulous region is short; in *Galeops,* a large edentulous region is present.
2) *The Proportions of the Face:* In *Galechirus,* the face is relatively long; *Galepus* and *Galeops* show a progressive reduction in the length of the face (Fig. 12).
3) *The Lower Jaw:* In *Galechirus,* the lower jaw is slender and the ventral border is concave; in *Galepus* and *Galeops,* a progressive decrease in the length of the jaw is seen and the ventral margin becomes straight (Fig. 12).
4) *Humerus:* In *Galechirus* and *Galepus,* the dorsal margin of the humerus is straight when seen in anterodorsal view. In *Galeops,* the proximal end of the humerus curves strongly dorsally.
5) *Ectepicondylar Foramen:* In *Galechirus,* a well-developed ectepicondylar foramen is present; in *Galepus,* this foramen is reduced; in *Galeops,* an ectepicondylar foramen is absent.

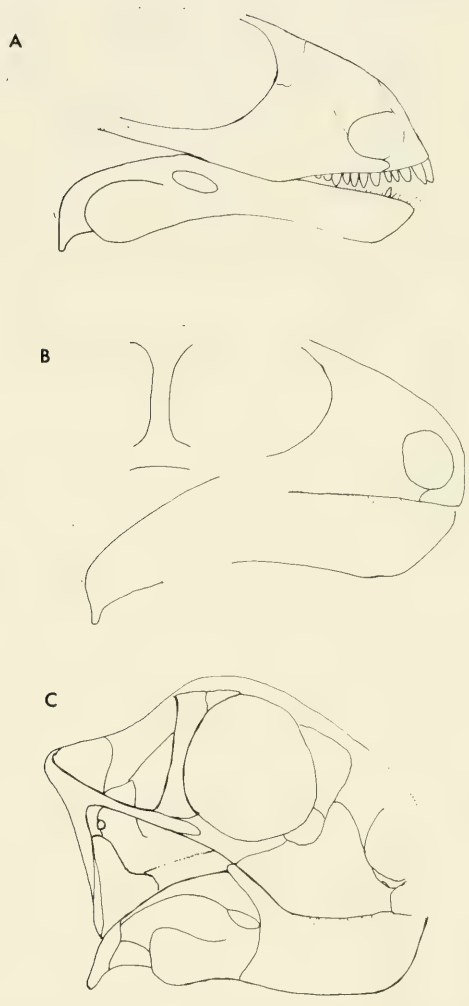


Figure 12. Reconstructions of the skulls of the dromasaurs. A) *Galechirus sholtzi;* B) *Galepus jouberti;* C) *Galeops whaitsi.* Not drawn to scale.

Since the most derived member of this sequence is the earliest, these three genera cannot represent successive stages in a single evolving lineage. Rather, they must be regarded as members of distinct grades of evolution in a single monopholetic radiation.

ACKNOWLEDGMENTS

I would like to thank Dr. R. L. Carroll of McGill University at whose suggestion this project was undertaken. Dr. M. A. Cluver provided silicone rubber casts of the specimens housed in the South African Museum. Drs. M. A. Cluver, A. W. Crompton, and R. L. Carroll read the manuscript and made many useful suggestions that led to its improvement. Drs. J. A. Hopson and H. R. Barghusen freely provided important information on the structure of the venjukoviamorphs. I would also like to thank Lillian Mahoney for proofreading the manuscript.

LITERATURE CITED

Baird, D. 1951. Latex molds in paleontology. Compass of Sigma Gamma Epsilon, **28:** 339–345.

———. 1955. Latex micro-molding and latex-plaster molding mixture. Science, **122:** 202.

Barghusen, H. R. 1976. Notes on the adductor jaw musculature of *Venjukovia*, a primitive anomodont therapsid from the Permian of the USSR. Ann. S. Afr. Mus., **69:** 249–260.

Barry, T. H. 1974. A new dicynodont ancestor from the Upper Ecca (Lower Middle Permian) of South Africa. Ann. S. Afr. Mus., **64:** 117–136.

Boonstra, L. D. 1965. The limbs and girdles of the Gorgonopsia of the *Tapinocephalus* zone. Ann. S. Afr. Mus., **48:** 237–249.

———. 1966. The girdles and limbs of the Dicynodontia of the *Tapinocephalus* zone. Ann. S. Afr. Mus., **50:** 1–11.

Broom, R. 1907. On some new fossil reptiles from the Karroo beds of Victoria West, South Africa. Trans. S. Afr. Phil. Soc., **18:** 31–42.

———. 1910. A comparison of the Permian reptiles of North America with those of South Africa. Bull. Am. Mus. Nat. Hist., **28:** 197–234.

———. 1912. On some new fossil reptiles from the Permian and Triassic beds of South Africa. Proc. Zool. Soc., **1912:** 859–876.

———. 1914. On the origin of mammals. Phil. Trans. Roy. Soc. Lond. B, **206:** 1–48.

Carroll, R. L. 1976. *Noteosuchus,* the oldest known rhynochosaur. Ann. S. Afr. Mus., **72:** 37–51.

Cluver, M. A. 1970. The palate and mandible in some specimens of *Dicynodon testudirostris* Broom & Haughton (Reptilia, Therapsida). Ann. S. Afr. Mus., **56:** 133–153.

———. 1975. A new dicynodont reptile from the *Tapinocephalus* zone (Karoo system, Beaufort series) of South Africa, with evidence of the jaw adductor musculature. Ann. S. Afr. Mus., **67:** 7–23.

Cox, C. B. 1959. On the anatomy of a new dicynodont genus with evidence on the position of the tympanum. Proc. Zool. Soc. Lond., **132:** 231–367.

Crompton, A. W., and N. Hotton III. 1967. Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida). Postilla, **109:** 1–51.

Hopson, J. A. 1969. The origin and adaptive radiation of mammal-like reptiles and nontherian mammals. Ann. New York Acad. Sci., **167:** 199–216.

Kitching, J. W. 1977. The distribution of the Karroo vertebrate fauna. Memoir 1. Bernard Price Institute for Paleontological research. Johannesburg, University of Witwatersrand, 131 pp.

Olson, E. C. 1962. Late Permian terrestrial vertebrates, USA and USSR. Trans. Amer. Phil. Soc. N.S., **25:** 1–225.

Romer, A. S. 1956. The Osteology of the Reptiles. Chicago, University of Chicago Press, 772 pp.

Romer, A. S., and L. I. Price. 1940. Review of the Pelycosauria. Geol. Soc. Amer. Spec. Pap. No. 28, 538 pp.

Romer, A. S., and D. M. S. Watson. 1956. A classification of therapsid reptiles. Bull. Mus. Comp. Zool., **114:** 37–89.

Watson, D. M. S. 1948. *Dicynodon* and its allies. Proc. Zool. Soc., **118:** 823–877.

MUS. COMP. ZOOL
LIBRARY
MAR 18 1985
HARVARD
UNIVERSITY

BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 30 JUNE 1982 NUMBER 466

SYSTEMATICS OF THE *MEXICANA* SPECIES GROUP OF THE COLUBRID GENUS *LAMPROPELTIS*, WITH AN HYPOTHESIS MIMICRY

WILLIAM R. GARSTKA[1]

ABSTRACT. Variation within the *mexicana* group of kingsnakes, genus *Lampropeltis* (Fitzinger), is discussed. Three species are recognized: *L. mexicana* (Garman), *L. alterna* (Brown), and *L. ruthveni* (Blanchard), which is added to the species group. *L. leonis* (Gunther) is placed in the synonymy of *L. mexicana*. Qualitative and quantitative characters of external and internal morphology are used to diagnose the taxa. Outgroup comparisons with other *Lampropeltis* and other colubrids indicate that *L. mexicana* is primitive relative to *L. alterna*. Evolution within the group and an hypothesis of mimicry to explain pattern polymorphisms are discussed.

L. alterna as interpreted here is restricted to areas north of the Anticline of Arteaga, Mexico and occurs throughout the Bolsón de Mapimí and north to the foot of the Guadalupe Mountains. *L. mexicana* is a montane and plateau form occurring on and to the south of the Anticline of Arteaga. *L. ruthveni* has been found in northwestern Michoacán and adjacent Querétaro in the transverse volcanic region. Sympatry is not recorded for the taxa.

INTRODUCTION

The kingsnakes allied with *Lampropeltis mexicana* (Garman) are relatively small (less than one meter) little-known snakes which inhabit the Chihuahuan Desert and adjacent areas. They occur from

[1]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. Present address: Department of Biological Sciences, University of Alabama in Huntsville, Huntsville, Alabama 35899.

northern Michoacán, Mexico, north to perhaps southern New Mexico. The taxa have been considered closely related and have been called variously a species group (Smith, 1942, 1944; Webb, 1961) or a species complex (Gehlbach and Baker, 1962; Gehlbach and McCoy, 1965; Gehlbach, 1967; Tanzer, 1970). The nominal taxa are *L. mexicana* (Garman), *L. thayeri* Loveridge, *L. greeri* Webb, *L. leonis* Gunther, *L. alterna* (Brown), and *L. blairi* Flury. These species have been considered as a unit because of the following shared characteristics: a light-edged red-centered black blotch, mottled speckling, distinct head, and long tail (Gehlbach and Baker, 1962). I also include in this group *L. ruthveni* (Blanchard) because it clearly fits these criteria, and is sympatric with *L. triangulum.*

The findings reported here suggest that the *mexicana* group consists of three species-level taxa which are distinctive in several character suites: *L. alterna* (including *L. alterna* and *L. blairi*), *L. mexicana* (including *L. mexicana, L. thayeri, L. greeri,* and *L. leonis*), and *L. ruthveni* (removed from the synonymy of *L.t. arcifera*).

The *mexicana* group is related closely to *L. triangulum* on the basis of shared hemipenial characters (Smith, 1942) and may also show close relationship to *L. pyromelana* and *L. zonata* when pertinent characters are more closely examined in those species. The *mexicana* group has been considered both as ancestral to the remaining species of *Lampropeltis* (Webb, 1961) and as the most derived species (Blanchard, 1921; Smith, 1942, 1944; Tanner, 1953). Data will be presented demonstrating that *L. alterna* is the most derived species in the group, and that both it and *L. ruthveni* are closely related to *L. mexicana.* Although the distribution of all three species appears to be presently patchy and perhaps relictual, this is not sufficient justification for considering them ancestral.

Four specimens of *Lampropeltis,* seemingly related to *L. mexicana,* were collected by the author in Coahuila and Nuevo León, Mexico, during 1975 and 1976. It was not possible to refer three of the four specimens to any presently recognized taxon when compared to the key in Webb (1961) and the descriptions in Gehlbach (1967). Comparison with reference material did not clarify the situation. Of the four specimens previously known from the vicinity of Galeana, Nuevo León (Gehlbach and McCoy, 1965; Gehlbach, 1967), one was identified as *L. mexicana thayeri,* one as *L.m. alterna,* and two as *L.m. thayeri* × *L.m. mexicana* intergrades. The only additional specimen from Nuevo León was the holotype of the obviously closely

related *L. leonis.* It was clear then that a revision of the goup and reidentification of the reference material was necessary.

One of the above specimens collected by the author (from San Lazaro, Coahuila) has a series of 24 laterally truncated body rings; thus it should have been classed as *L.m. thayeri* (Webb, 1961). However, in comparison with the type specimen of *thayeri* and a living specimen quite like the type, this Coahuila specimen was clearly different. The head was much more triangular, as has been noted for *alterna* (Brown, 1901; Gehlbach, 1967); the number of ventral scales was nearly 20% greater than reported for *thayeri,* and the iris was silver-grey, like specimens from Texas and unlike the gold-brown iris of animals collected in the mountains of Nuevo León. Living specimens collected in the mountains of Durango, Mexico, were similar in these three characters with those from Nuevo León, and were likewise similar to specimens from Querétaro, except in ventral scale number.

The specimens recently collected in Querétaro, Mexico, posed another problem, as they closely resembled the single previous specimen identified as *L. ruthveni* (Blanchard, 1921), which had been synonymized (Williams, 1978) with *L.t. arcifera.* These specimens share many of the same features of *L. mexicana,* and indeed are distinguishable only on ventral scale number from some *L. mexicana* from Nuevo León. They are clearly not *L. triangulum nelsoni* nor *L.t. arcifera,* with which they are sympatric; both subspecies of *L. triangulum* have been collected (Williams, 1978) in the valleys that surround the montane area where the *ruthveni* were collected. Therefore an initial hypothesis of three valid taxa, *alterna, mexicana,* and *ruthveni,* was considered, and characters were analyzed within that framework.

The most striking feature of kingsnakes is their often brilliant color and pattern. Color and pattern have been relied upon exclusively in diagnoses of the species of *Lampropeltis* (Blanchard, 1920, 1921; Gehlbach, 1967; Smith, 1942; Webb, 1961) and the subspecies of *L. triangulum* (Williams, 1978). The extreme variability of color and pattern among individuals in the *mexicana* group and the similarity of the patterns of *ruthveni* and some *mexicana* with some subspecies of *triangulum* makes using only this character untenable.

Color and pattern variability is also well documented in Texas *alterna* (Gehlbach and Baker, 1962; Gehlbach and McCoy, 1965; Gehlbach, 1967; Tanzer, 1970; Miller, 1979). There is a gradation of

patterns from extremes of more than 17 narrow rings with alternating dots (*alterna*) to a low number (9–17) of major bands with no alternating reduced markings (*blairi*). Tanzer (1970) reported a brood from an *alterna* female which contained both *blairi* and *alterna* offspring. Melanism is also known in both *alterna* (Miller, 1979) and *mexicana*.

The morphological characters examined in this study are: 1) lepidosis, 2) color and pattern, including color of the iris, 3) osteology of the skull and vertebrae, and 4) hemipenes. The variation in these characters is analyzed in *mexicana, ruthveni,* and *alterna,* and each taxon is compared with its respective sympatric *triangulum* population. The three taxa are redefined, and a hypothesis of relationship and of selection pressures leading to evolution within the group is presented.

MATERIALS AND METHODS

Specimens

Both preserved and living specimens including all age classes were examined. Embryo and hatchling specimens were examined and used in ontogenetic comparisons with adults. Living snakes were sexed by the method of Laszlo (1975) using probes manufactured by J & M Specialty Parts. All living specimens in the author's collection will be deposited in the Museum of Comparative Zoology. Wild caught specimens only were used in the character analysis as captive bred animals cannot be considered as statistically independent samples.

External Morphology

Scale counts recorded included ventrals (method of Dowling, 1951), subcaudals, infralabials, supralabials, temporals, and dorsal scale rows at mid-body (V method of Peters, 1964). The location of the umbilical scar on hatchling specimens was noted. Dissected and everted hemipenes of each taxon were examined. Statistical analysis of data used methods from Sokal and Rohlf (1969). All sample means indicated in the text are followed by $\pm$ one standard error of the mean.

X-Rays

Radiographs of preserved specimens were taken on an F.E. Faxitron X-ray machine using Kodak Industrex R film. Measurements of

five thoracic vertebrae posterior to #20 were taken from each specimen radiographed. Coiling of preserved specimens prevented examination of the same five vertebrae on every animal. Measurements and terminology of the vertebrae are from Johnson (1955a, 1955b) and Auffenberg (1963). Comparisons were made between replicate radiographs of the same vertebrae, and between measurements from a prepared skeleton and radiographs of the same vertebrae to be confident of accuracy and precision. Differences were less than 3%. Dorsoventral radiographs of heads and measurements of the length and width of the skull at various levels were also taken. Individual osteological elements of the skull were not examined. Comparisons were again made of three sets of duplicate radiographs, and the differences were less than 2%.

Field Work

During 1972, 1973, and 1975 trips were made to the Chihuahuan Desert areas of Texas, principally to Brewster, Presidio, and Val Verde counties. During 1974, 1975, 1976, 1979, and 1980 trips were made to various localities in Mexico. Collection of living specimens provided information on the ecology and extent of distribution of the group.

ANALYSIS OF CHARACTERS

Lepidosis

There is a marked difference in the numbers of ventral scales of the three taxa (see Table 1 and Fig. 1). A one-way ANOVA shows that there is significant heterogeneity of mean ventral scale number among taxa ($F = 85.3$ at 2/83 df, $p < 0.005$). In a Student-Newman-Keuls test of differences between ranked pairs of means, all differences are significant at the 1% level. In order to be assured that distinct populations were sampled, the distributions were tested for normality. The individual taxon distributions are not different from normal by the Kolmogorov-Smirnov cumulative test (D [*alterna*] = 0.09, critical value = 0.29, $\alpha = 0.01$; D [*mexicana*] = 0.07, critical value = 0.30, $\alpha = 0.01$; D [*ruthveni*] = 0.13, critical value = 0.30, $\alpha = 0.01$). The total distribution was tested for normality and was found to be significantly different from normal (D = 0.27, critical value = 0.18).

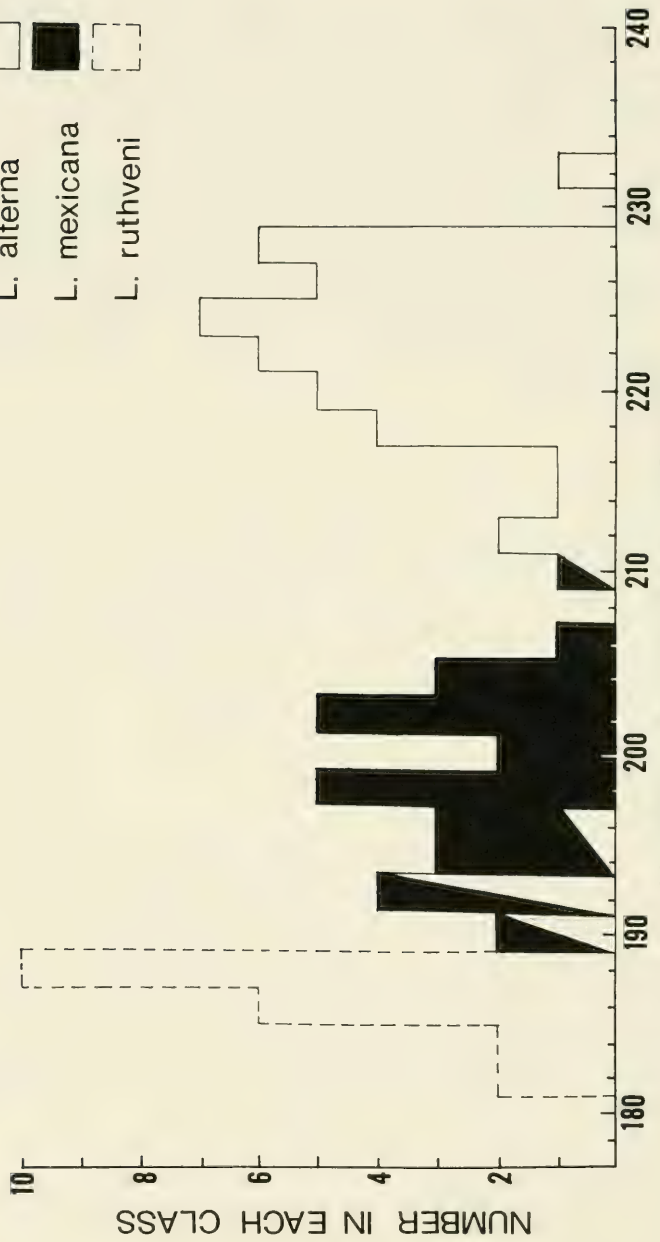


Figure 1. Ventral scale counts of the three species in the *mexicana* group.

The variation among the ventral scale means of *alterna, mexicana,* and *ruthveni* appears as a north to south cline. This variation, however, is not clinal within a taxon, and the differences among taxa are stable in captive-bred animals. Clinal variation in ventral scale number has been documented for *Coluber constrictor* (Auffenberg, 1955) and *Lampropeltis triangulum* (Williams, 1978). In both taxa the change is gradual, with counts high in the south, low in the north. The effects of differing temperatures of incubation on scale counts (Fox *et al.,* 1961) could explain that situation, although no experimental evidence was given for either species.

The geographic distribution of ventral scale numbers within each taxon appears random (Table 2). The southernmost specimens of *alterna* from just north of Saltillo, Coahuila (USNM 110819) and from near San Antonio, Durango (TCWC 36892), have 223 and 218 ventrals, respectively. The northernmost *mexicana* specimens, three from the Rio Mimbres area of Durango (UCM 21061 and 2 Garstka collection) and one from the Anticline of Arteaga near Los Lirios, Coahuila (ITESM uncataloged), have 203, 202, 204, and 190, respectively. The Los Lirios *mexicana* has the lowest ventral number of any *mexicana* examined.

The hypothesis that the north to south cline in ventral scale counts may be a result of differing incubation temperatures was examined by incubating two clutches of *mexicana* eggs and one clutch of *alterna* eggs in the same container at the same time (*alterna:* 3 August–23 October; *mexicana:* 14 July–25 September; 28 June–18 September 1977). The same means of ventral counts are *alterna* = 218.5 ± 2.50 (N=2); *mexicana* = 204.6 ± 1.45 (N=10), and the difference is significant ($t = 8.47$, $p < 0.001$). In an additional sample of captive-bred *alterna* (218.8 ± 0.38, N=40) and captive-bred *mexicana* (201.6 ± 7.87, N=7), the difference is also significant ($t = 18.28$, $p < 0.001$). The conditions and dates of incubation for the latter sample are not known.

Juvenile specimens usually possess an umbilical scar. The number of ventral scales anterior to the scar is 170.9 ± 1.48 for 11 *mexicana* and 190.0 ± 1.69 for 12 *alterna* ($t = 12.98$, $p < 0.001$). The length of the scar is the same in both taxa; the mean lengths in the samples are 4.5 ± 0.25 scales for *mexicana* and 5.0 ± 0.37 scales for *alterna* ($t = 1.25$, $0.3 > p > 0.2$). No sex differences were noted. The single juvenile *ruthveni* (KU 155528) had no visible scar.

Table 1. Diagnostic characters of the *mexicana* group and sympatric subspecies of *Lampropeltis triangulum*.

		Character				
		ventrals		body rings		
Taxon	N	range	$\bar{X} \pm SE$	range	$\bar{X}$	snout color
L. alterna	30	211-230	221.3 ±0.8	9-32	16	variable, see text
L. mexicana	29	190-211	198.5 ±1.0	23-46	32	variable, see text
L. ruthveni	28	182-196	188.6 ±0.6	23-34	29	black to posterior of parietals, or with some red or white flecks
L. t. annulata[1]	40	181-207	194.7 ±1.1	14-22	18	black to center of parietals
L. t. arcifera[1,2]	18	196-220	210.1 ±1.6	17-27*	24	variable, from black to *nelsoni* condition
L. t. celaenops[1]	12	170-194	183.4 ±2.6	17-25	22	black to center of parietals or with white flecks
L. t. nelsoni[1,2]	23	203-221	215.0 ±2.4	13-18*	16	white to posterior of prefrontals, then black, or with black flecks
L. t. ssp. nov.[2]	6	189-201	196.2 ±1.7	14-22**	21	black to posterior of parietals, or with white flecks

[1]data from Williams (1978)
[2]data from H. Quinn (personal communication)

*some red rings split with black mid-dorsally
**most red rings split with black mid-dorsally

Table 2. The relationship between latitude and number of ventral scales in the *mexicana* group.

Degrees North Latitude	Number of Ventral Scales		
	alterna	*mexicana*	*ruthveni*
30-32	221.5 ±1.7(N=8)		
28-30	222.3 ±1.1(18)		
26-28	214.0 ±1.0(2)		
24-26	220.5 ±2.5(2)	200.9 ±1.6(11)	
22-24		196.3 ±1.0(18)	
20-22			188.6 ±0.7(26)
18-20			188.0 ±0.0(2)

The pattern of ventral scale counts in these taxa is clearly different from that of each sympatric *triangulum* variety (Williams, 1978). *L. triangulum celaenops* and *L.t. annulata* are sympatric with *alterna, L.t. nelsoni* and *L.t. arcifera* with *ruthveni,* and there is apparently no *triangulum* sympatric with the montane *mexicana.* The ventral scale counts of Williams' (1978) and Quinn's (in preparation) samples of *celaenops, annulata, arcifera, nelsoni,* and a new subspecies can serve to distinguish each species of the *mexicana* group from its sympatric *L. triangulum* subspecies (Table 1.)

There is no clear separation of the taxa in other scale characters. The uppermost preoculars in most *mexicana* and *ruthveni* extend onto the top of the head to or nearly to the frontal, whereas in *alterna* they rarely do so. There is much variability and overlap between taxa in the number and arrangement of the temporal scales. There is also no differences among taxa in numbers of labial scales, subcaudals, or dorsal scale rows, and all specimens examined possess a loreal (Table 3).

Color Pattern

The variable head and snout markings of this group can be grouped into four categories: I) asymmetric spot or blotch markings without red, II) snout evenly black to the middle or posterior of the parietals, with or without a red infusion, III) a red-centered, three-lobed cloverlike marking with the anterior lobe across the frontal or usually the prefrontals, and IV) a similar three-lobed marking, without red, that can have the anterior lobe either split to form a double Y, detached, or enlarged and subrectangular (Fig. 2). None of these categories is exclusive to any taxon, but most *ruthveni* are category II, and most *alterna* are category I. The head markings connect to the nuchal blotch only in some *mexicana.* The nuchal blotch of *mexicana* and *alterna* is usually light-centered and can be split longitudinally. Postocular stripes are usually present in all taxa (absent in UCM 21061, a *mexicana*), but may be reduced or obscured, as occurs in category II.

All living specimens examined of *alterna* have a distinctive silver-grey iris; *mexicana* and *ruthveni* have a golden-brown iris. Other *Lampropeltis (getulus, triangulum, pyromelana,* and *zonata)* examined also have a golden-brown iris.

Table 3. Scale count variation in the *mexicana* group.

Scale Character	Range of Scale Counts		
	alterna	*mexicana*	*ruthveni*
ventrals	211-230	190-211	182-196
subcaudals	56-67	51-65	49-57
dorsal scale rows	23-27	21-25	21-25
temporal scale rows	2-4	2-4	2-4
number of scales in anterior temporal row	2-3	1-3	1-2
number of scales in posterior temporal row	3-5	3-5	3-5
supralabials	7-8	7-8	6-8
infralabials	9-11	8-11	8-9

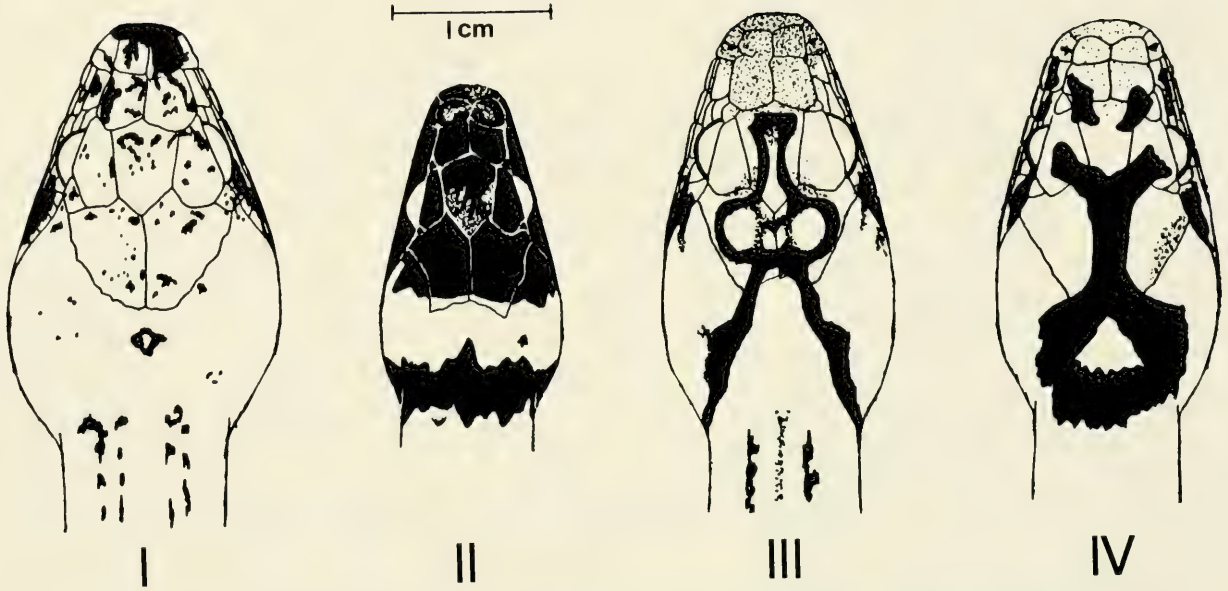


Figure 2. Categories of head and snout markings in the *mexicana* group. I) *L. alterna* (USNM 110819); II) *L. ruthveni* (in Garstka collection); III) *L. mexicana* (MCZ24976); IV) *L. mexicana* (in Garstka collection).

The number of primary, usually red-centered, body markings varies considerably and is not by itself indicative of any taxon (Table 1). The *blairi* form of *alterna* has the fewest primary markings (9–17).

The 47 offspring produced in ten broods by one male and two female *mexicana* collected from a single site near San Juanito, Nuevo León, are variously ringed, blotched, or spotted. All possible variants of the dorsal head pattern occur in these offspring, and ground color ranges from lemon-yellow through various shades of brown, orange, and grey. The blotches vary in number from fewer than 20 to more than 40, and in shape from spots to rings extending around the body. The number of body bands falls within the ranges of all the forms except *blairi.* In some, alternating reduced markings occur in one or several rows. One specimen has red only in the nuchal blotch. Thus, neither number, level of truncation (Webb, 1961) or alternating reduction (Blanchard, 1920, 1921; Smith, 1942) of body bands are diagnostic characters. The local variability characteristic of *mexicana* and *alterna* is not present in any *triangulum* subspecies, nor are alternating reduced markings recorded for any *L. triangulum.*

Ventral pigmentation ranges from nearly entirely black to nearly entirely background color in *alterna* and *mexicana.* The *ruthveni* examined most commonly have rings which extend around the body; this also occurs with the anterior rings in some *mexicana.* The venter of *alterna* and *mexicana* can also be checkered in black and background color as in *L.t. triangulum* and *Elaphe guttata* (see figure in Smith, 1942, pp. 202–203), and some *ruthveni* have a checkered red pattern ventrally.

A ventrolateral expansion of the first (anteriormost) tail blotch with red extending onto (usually across) the subcaudals is characteristic of *mexicana.* This character is not evident in any of the *alterna* examined. The underside of the tail of one specimen of *mexicana* (BMNH 1946–1–4–10) has red infused anteriorly in a longitudinal black line. The tails of the *ruthveni* examined have a ringed condition similar to *mexicana;* however, the first tail ring is not usually widened ventrolaterally. The anterior tail rings are not different from body rings in any of the *L. triangulum* subspecies.

The *L. triangulum* subspecies sympatric with each taxon can be distinguished by a combination of color patterns and scale characters from the sympatric member of the *mexicana* group (Table 1).

The snout color and symmetric body annuli of *ruthveni* make these animals easily distinguishable from the sympatric *nelsoni*. Similarly, the high number of annuli of *celaenops* and *annulata* are different from the usually few annuli of the ringed or saddled *blairi* form of *alterna*. In the other cases, some combination of color pattern with ventral scale number serves to diagnose members of the *mexicana group*.

Skull

Data from dorsoventral radiographs of similarly sized, adult *alterna* (N = 7) and *mexicana* (N = 12) were compared to quantify the observation of a more triangular head shape in *alterna*. The premaxilla to occipital condyle length, the width of the maxilla at

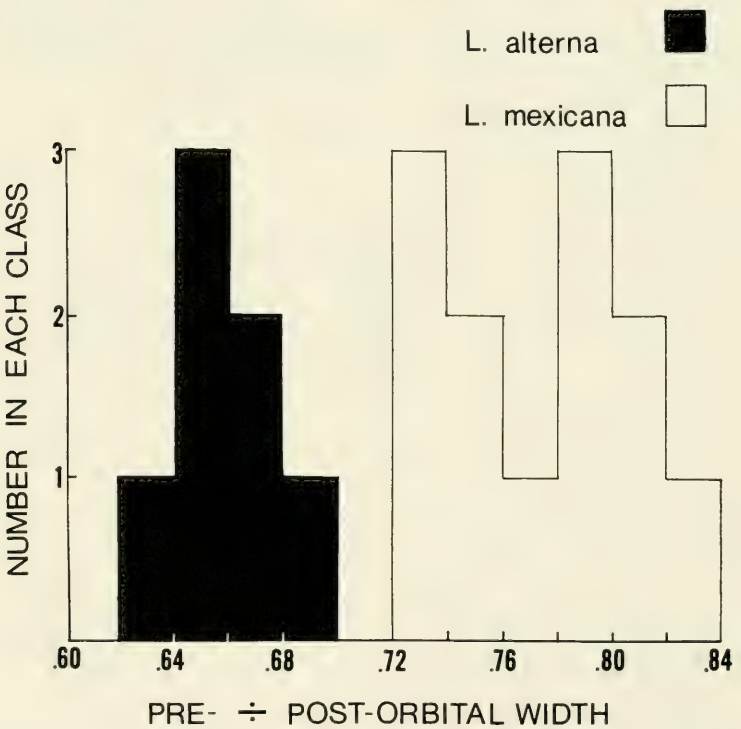


Figure 3. The ratio of pre-orbital and post-orbital width of *L. alterna* and *L. mexicana* adults.

the prefrontals, the least width of the frontals, the maximum widths across the post-orbitals, across the supratemporals, and across the quadrates were measured. The ratio of preorbital to postorbital width was used to quantify triangularity of the skull, as that should be least influenced by kinesis. The mean ratio of the *alterna* sampled is 0.66 ± 0.007 and of the *mexicana* sampled is 0.77 ± 0.010. They are significantly different ($t = 7.343$, $p < 0.001$) (Fig. 3). The single *ruthveni* adult examined for this character (USNM 46558) has a ratio of 0.74.

Additionally, ten juveniles each of *alterna* and *mexicana* were compared for this character. The mean ratio of the sample of *mexicana* juveniles is 0.74 ± 0.007, with one specimen outside the range of variation of the adults, in the direction of *alterna*. In the sample of juvenile *alterna*, five are outside the variational range of adult *alterna* in the direction of *mexicana*, and the mean is 0.69 ± 0.008. Thus the two taxa are more similar as juveniles, and, importantly, are more like *mexicana* than *alterna* as juveniles. This indicates that there is differential growth to the adult stage in *alterna*.

Adults of other species of *Lampropeltis* were also examined in outgroup comparison for this character. *L. triangulum amaura* and *L.t. polyzona* both had a preorbital to postorbital ratio of 0.77, a single *L. pyromelana* had a ratio of 0.73, and a single *L. calligaster* had a ratio of 0.73. Thus, it appears that the lesser triangularity of the skull in the *mexicana* condition is not only the common condition for juveniles, but also for other *Lampropeltis*.

Vertebrae

Eight or more individual thoracic vertebrae (Johnson, 1955a, 1955b; = first precaudal series, Auffenberg, 1963; = lumbar series, Bullock and Tanner, 1966) prepared from each of eight adult specimens of *alterna* and four adult *mexicana* were examined. X-rays in lateral and dorsoventral aspect of an additional three adult and five juvenile *alterna* and six adult and nine juvenile *mexicana* were also examined. No *ruthveni* vertebrae were available. None of the commonly used measures (Johnson, 1955a, 1955b) or ratios (Auffenberg, 1963) showed any significant difference between adults of the two taxa. The amount of individual variation in qualitative appearance of the vertebrae is substantial, however, even in the small sample examined; because of the lack of descriptions of the range of

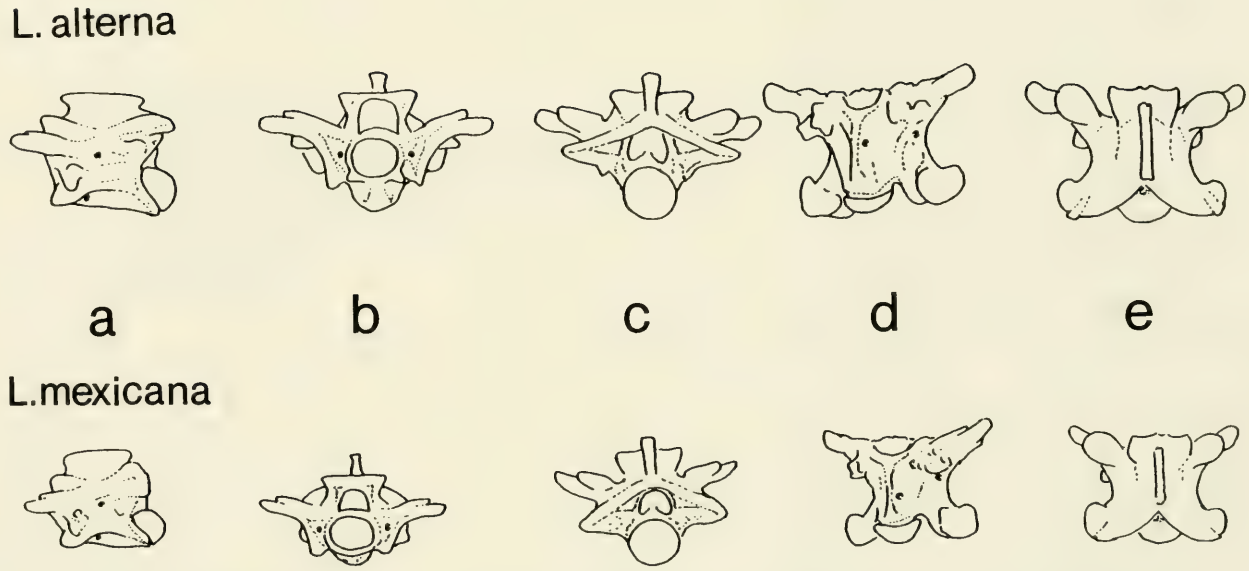


Figure 4. Vertebrae of *L. alterna* (MCZ 157764) and *L. mexicana* (MCZ 157766). a) left lateral; b) anterior; c) posterior; d) ventral (angled to right); and e) dorsal aspects.

individual variation of colubrid vertebrae, and the importance of vertebral characters in the systematics of fossil forms, an analysis of the vertebrae follows (Fig. 4).

The neural spine may be blunt or pointed, and in all individuals of *mexicana* examined it overhangs both anteriorly and posteriorly. In lateral X-ray the neural spine of a single *alterna*, USNM 110819, appears to not overhang anteriorly. The zygosphene is crenate to convex from above and usually has a broad shallow notch. In anterior aspect the dorsum of the neural arch is flattened or slightly arched and is thinned centrally; the sides are obtusely angled, forming a dorsolateral articulating surface. The dorsal articulating surfaces of the anterior zygapophyses are ovoid to reniform and their lateral accessory processes can be blunted or pointed, directed laterally or upward, and if upward, may be curved. The processes may be rounded to dorsoventrally compressed, and if compressed, may be tilted to be parallel to the centrum. The cotyle may be round to ovoid and if ovoid, may have accessory flanges or fillets, usually ventrally, that make it appear rectangular. The parapophyses may or may not project ventral to the cotyle and may be projected anteriorly. The paradiapophysial articulating surfaces are in the form of a figure-8 with the upper portion larger and directed anteriorly, and the lower surface directed laterally to posteriorly. There is a small foramen on the parapophyses lateral to the cotyle on each side approximately at its midline. The haemal keel is usually ridgelike, though it may be flattened or absent. The subcentrum ridges are straight to slightly concave. There are two pairs of subcentrum foramina, one pair on either side of the haemal keel and the other more lateral and dorsal, just ventral to the lateral flange of the body. The condyle is oblique. In posterior view, the neural arch is rounded dorsally and flattened ventrally with a central ventral ridge. There are also lateral minor ridges extending the length of the canal on either side approximately one third of the distance superior to the base. The ventral exterior articulating surfaces of the posterior zygapophyses are ovoid to reniform with the long axis perpendicular to the centrum. The medial articulations that match the dorsal zygosphene corners, the zygantra, appear as enlarged triangular holes lateral to the neural arch. There are small projections posterior and lateral to the posterior zygapophyses just dorsal to the ventral articulating surfaces.

Juvenile vertebrae present quite a different appearance from those of adults, which is most noticeable in the proportionally larger neural canal. The ratio of length of the centrum to width of the neural canal in a sample of three adult *mexicana* is 2.1 ± 0.10, of three adult *alterna* is 2.3 ± 0.08, and of eight juvenile *mexicana* is 1.2 ± 0.03. The neural spine is also proportionally higher. The ratio of length to height of the neural spine of a sample of three *mexicana* adults is 2.4 ± 0.34 and of three juvenile *mexicana* is 1.5 ± 0.09. The juvenile *alterna* sampled had vertebrae insufficiently ossified to obtain the measurements for comparison. Since nervous tissues have grown most in relation to other tissues at birth, and since ossification is incomplete then, these differences are to be expected.

The thoracic vertebrae of *L. triangulum* differ from *alterna* and *mexicana* in the form of the zygosphene which is arched rather than flattened (Brattstrom, 1955; Auffenberg, 1963). All of the tricolored kingsnakes examined (*L. triangulum, L. pyromelana, L. zonata, L. alterna,* and *L. mexicana*) share the single foramina lateral to the cotyle and the two pairs of subcentrum foramina. *L. getulus* and *L. calligaster,* however, have two pair of foramina adjacent to the haemal keel and a pair of foramina on each side of the cotyle.

Hemipenes

Previous workers (Smith, 1942; Gehlbach and Baker, 1962) have reported on the hemipenes of *alterna* and *mexicana,* and allied the taxa with *L. triangulum* on the basis of overall similarity of gross structure. The hemipenes of three adult *mexicana,* five adult *alterna,* and two subadult *ruthveni* have been examined. They are uniformly longitudinally flounced proximally, then abruptly spinulate, quickly grading into slightly spinulate fringed calyces. The sulcus is single and terminates laterally on the very slightly bilobed organ. This morphology is similar to that of *L. triangulum.*

The spination on the hemipenes is clearly different among the *mexicana* group, however (Fig. 5). The spines of *mexicana* are very slightly recurved and are about 0.4 mm long. They appear diamond-shaped in cross section and are tightly packed on the organ. The spines of *alterna* and *ruthveni* are also recurved but are longer, to approximately 0.8 mm in *alterna* and 0.6 mm in *ruthveni,* and the supporting tissue makes them appear more ovoid or flattened in cross section. The spines also appear to be fewer in number in these

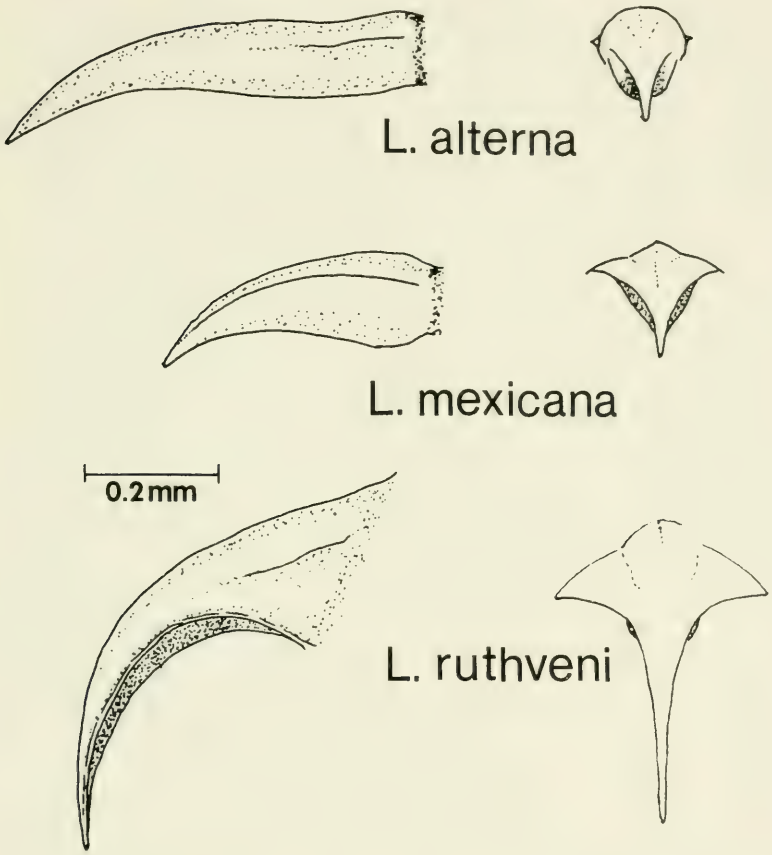


Figure 5. Hemipenial spines of *L. alterna, L. mexicana,* and *L. ruthveni.* Lateral (L) and distal (R) aspects.

taxa than in *mexicana.* The spines of both *ruthveni* examined are more strongly recurved than those of both *mexicana* and *alterna.*

Ecology

The distribution of the entire *mexicana* group has been characterized as xeric to subhumid (Gehlbach and Baker, 1962) and roughly corresponds to the limits of the Chihuahuan Desert as described by Morafka (1977) (Fig. 6).

L. alterna is found within the Chihuahuan Desert, usually in association with typically desert floral elements such as *Prosopis* and *Larrea* (Jameson and Flury,1949; Mecham and Milstead, 1949; Worthington, 1974). All known localities are within or north of the Bolsón de Mapimí. Specimens collected in the Chisos Mountains, Brewster County, Texas (Murray, 1939) and near Saltillo, Coahuila, Mexico (Smith, 1941) were found in rock crevices, though the species appears to be primarily nocturnal (Miller, 1979).

L. mexicana seems to be limited, except for CM 59980, to forested mesic areas peripheral to the desert, but with xerophytic vegetation such as *Echinocactus* and *Ariocarpus.* At *mexicana* localities in Nuevo León, San Luis Potosí, and Durango, Mexico, the vegetation may be termed "mesic to arid oak-pine forest" (J. Henrickson, personal communication), with the following dominant plants in common at the three localities: *Pinus cembroides, Quercus* sp., *Juniperus* sp., *Buddleja cordata,* and *Bouvardia ternifolia.* The author has collected specimens in rock crevices, under stones in an arroyo, and active on the road at night.

L. ruthveni is presently known from the northeastern portion of the trans-volcanic region in a habitat very similar to *mexicana.* In the vicinity of Amealco, Querétaro, Mexico, *ruthveni* are locally abundant in areas with scattered patches of *Quercus*-dominated woodland along arroyos and on hilltops. *Bouvardia* is common here as well. All recent collections have been of animals either in crevices or diurnally active.

Both *mexicana* and *ruthveni* appear to be more mesic species than *alterna,* occurring in more temperate forested areas. However, CM 59980 was collected in a desert area with stunted *Larrea,* cacti, and short grasses (D. Morafka, personal communication). The elevation of this rocky area is over 2,000 m, and while it is surrounded by a sandy plain, it is also closely adjacent to mesic upland areas. Many similar hilly areas in the vicinity have been deforested in recent times (T. Wendt, personal communication) and the area may have been woodland as recently as 100 years ago. *L. alterna* may also occupy upland (Worthington, 1974) or riparian habitats within the desert; however, it appears to be primarily a desert species. The higher ventral scale numbers of *alterna* may indicate adaptation to a desert environment, as Klauber (1941) found a correlation of higher ventral counts in desert habitats and lower counts in more humid coastal habitats in 12 of 13 taxa tested.

DISCUSSION

Phylogeny

Underwood (1967) considered *Lampropeltis* as derived from *Elaphe* on the basis of similarity of a long intrapulmonary bronchus, a series of skull characters, presence of similar scale tubercles, similar arrangement of pits on the head, and similar paired pits on trunk scales. The characters that define *Lampropeltis* as a group distinct from *Elaphe* are the entire anal scale and the unkeeled dorsal scales. Minton (1976) and Minton and Salanitro (1972) discussed the phylogeny of colubrids, based on the immunoelectrophoretic analysis of serum proteins and found that both *E. guttata* and *L. getulus* have the same degree of difference from *E. obsoleta.* Karyological evidence also demonstrates this similarity to *Elaphe.* A karyotype of 2N = 36 (16 macrochromosomes and 20 microchromosomes) has been reported for *L. getulus, calligaster,* and *alterna,* as well as for most *Elaphe (E. subocularis* is an exception) (Bury, *et al.* 1970; Baker, *et al.* 1972). This close relationship between *Lampropeltis* and *Elaphe* is also substantiated by vertebral morphology. The form of the neural spine and the arrangement of the vertebral foramina are similar in *L. getulus, L. calligaster,* and *Elaphe.*

All of the tricolored kingsnakes (*alterna, mexicana, pyromelana, ruthveni, triangulum, zonata*) share grossly similar derived hemipenial (Smith, 1942) and vertebral character states that are unlike those of the remaining species in the genus, *L. calligaster* and *L. getulus,* which are in turn similar to each other and to *Elaphe* (Cope, 1898).

Captive-breeding experiments (Miller, 1979; Tryon and Garstka, in preparation) have produced *alterna* × *mexicana, pyromelana* × *alterna,* and *pyromelana* × *zonata* hybrids. None of these species will mate with any *triangulum* subspecies tested in captivity. This can be taken as tentative evidence of their relationships. Therefore, it appears that all the tricolored kingsnakes share a common ancestor, and that the *mexicana* group forms a logical unit within that lineage, perhaps most closely related to *pyromelana* and *zonata.* Within the *mexicana* group, *alterna* is the most derived species, as shown by its iris color and head shape. These characters suggest that *alterna* is the most derived species within the genus as well (Fig. 6).

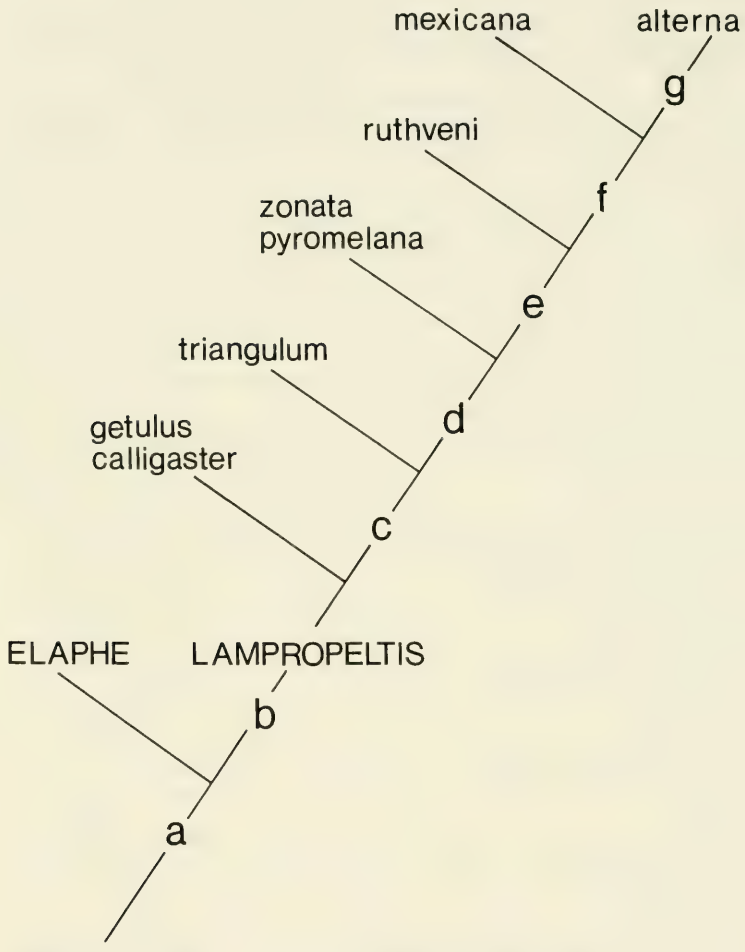


Figure 6. Hypothesis of relationship within the genus *Lampropeltis*. Derived character states uniting the taxa are: a) paired pits on trunk scales, long intrapulmonary bronchus; b) entire anal scale, unkeeled dorsal scales; c) single paired foramina lateral to hemal keel and cotyle, hemipenes flounced proximally and spinulate distally, pattern in three colors including red; d) behavioral traits in male aggression and reproduction; e) light-edged, red-centered blotch; f) alternating reduced markings possible; and g) grey iris, "triangular" skull.

The data presented here suggest that the three taxa hypothesized, *L. mexicana, L. alterna,* and *L. ruthveni,* are distinct morphological species. However, the taxa are allopatric, as are the two apparently most closely related species, *L. pyromelana* and *L. zonata.* Therefore the allocation of species status must still be regarded as an hypothesis until appropriate species borders or contact zones are established.

The species borders of *mexicana* and *alterna,* that is, the Anticline of Arteaga and the uplands of central Durango at the periphery of the desert, should be further collected. The presence of *alterna* at the base (USNM 110819) and *mexicana* (ITESM uncataloged) at the top of the Anticline of Arteaga indicate a high probability of a contact zone. Southern San Luis Potosí, Guanajuato, and northern Michoacán including the Sierra de Santa Rosa (Duges, 1897) and the escarpment of the basin of the Río Lerma should be explored as well for a species boundary or area of intergradation as this is between the localities of *mexicana* and *ruthveni.* Finally, the mountainous area of northern Durango north of Otinapa and west of Santiago Papasquiaro and the upper reaches of the Ríos San Juan and Verde need investigation. There are no kingsnakes known from that large area between the localities of *mexicana* and *pyromelana* (Taylor, 1940).

In addition, small sample sizes of some of the Mexican Plateau subspecies of *triangulum* make it difficult to determine the extent of sympatry, especially with *ruthveni,* and make comparisons difficult. More collections from that area, and revision of the genus or at least of the tricolored group, are necessary before the relationships among the various taxa can be better understood.

Variation and Selection of Color and Pattern

Many explanations of the significance of color and pattern in snakes have been proposed (see review by Jackson *et al.,* 1976). Aposematism, to warn potential predators, has been proposed as an explanation of bright colors on venomous snakes (Goodman and Goodman, 1976; Gehlbach, 1972; Smith, 1969). Mimicry of coral snakes by nonvenomous forms has been discussed extensively (Smith, 1969; Gehlbach, 1972; Greene and Pyburn, 1973; Echternacht, 1973; Hecht and Marien, 1956) as an explanation for the brightly colored rings on many snakes. Crypsis on broken back-

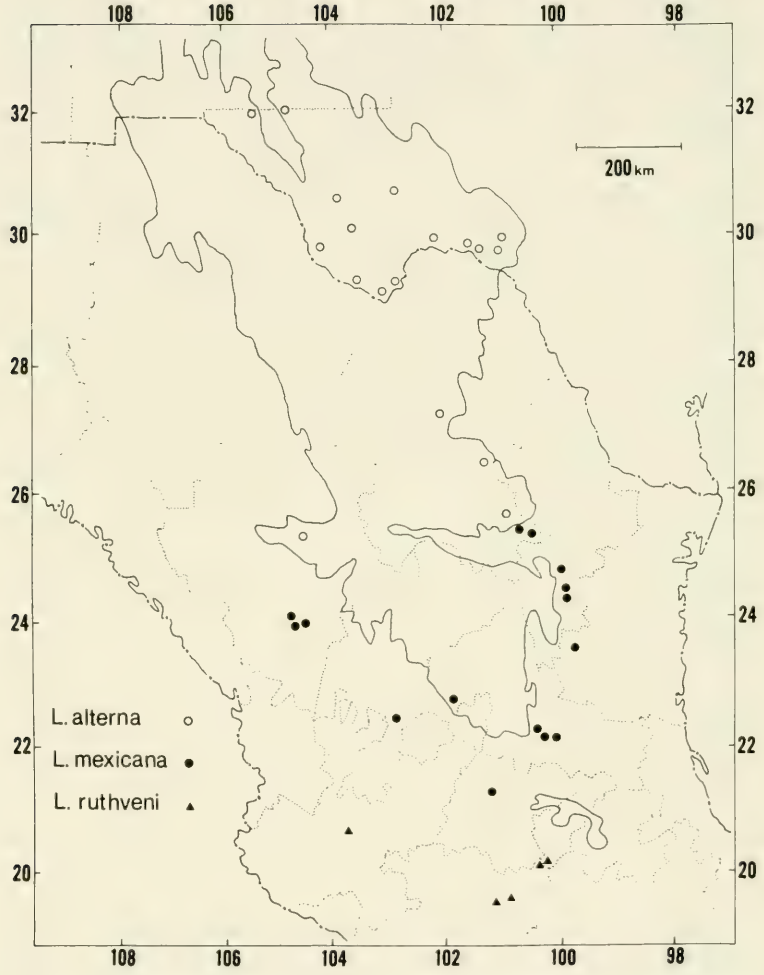


Figure 7. Distribution of the species in the *mexicana* group. State boundaries are shown as a dotted line, national borders as a broken line, and the extent of the Chihuahuan Desert (after Morafka, 1977) as a solid line. The Anticline of Arteaga is the band of mountains extending into the desert across southern Coahuila at about latitude 25° N. North of that is the Mapimian portion of the desert, and south of the Anticline is the Saladan portion of the desert (Morafka, 1977). Symbols denote only localities and not numbers of specimens.

grounds (Pough, 1976; Brattstrom, 1955), or lack of crypsis on a unicolored background (Camin and Erhlich, 1958) have also been cited to explain the presence or absence of a ringed or blotched pattern.

Gehlbach (1972) reported experimental evidence that self-mimicry, that is, the coral snake behavior of flipping the tail over, thwarted predation by coatimundis (*Nasua*) and peccaries (*Tayassu*). This effect was enhanced if the rubber models were painted aposematically. Evidence of the effectiveness of coral snake mimicry has been provided by experiments offering striped and ringed stick models to naive captive-raised motmots (*Eumomota superciliosa*) (Smith, 1975). The birds responded to red and yellow ringed models by avoidance and, in some cases, alarm notes.

L. mexicana and *L. alterna,* even though they may be brightly colored, do not look very much like coral snakes. Gans (1961) discussed an hypothesis of mimicry in *Dasypeltis,* a small nonvenomous snake that eats eggs of birds large enough to eat it. He demonstrated a correspondence of pattern between *Dasypeltis* and the local possible viperid models over its entire range. The pattern of the particular similar-sized viper in its range was mimicked. Therefore, the distribution of venomous snakes of the same general size and habits as *Lampropeltis,* and occurring within the range of the *mexicana* group, was examined. Crotaline models were considered, as the fine dark speckling on the scales lends an illusion of texture to the smooth-scaled *Lampropeltis.*

Agkistrodon mokeson pictigaster occurs in Texas west through the Big Bend region, but west of Val Verde County occurs only in the vicinity of permanent water sources. *Crotalus lepidus* is found throughout the range of *alterna* and is present in the same microhabitat. *Crotalus lepidus,* with its alternating broken pattern, can easily be mistaken for *alterna.* A similar pattern is also seen on *Trimorphodon* from west Texas. *Micrurus fulvius* is found in Texas west to Val Verde County.

The variation in Texas *alterna* could be a function of multiple models, the *blairi* form of *alterna* being a mimic of *Agkistrodon.* The relative constancy of pattern in *alterna* outside of the range of *Agkistrodon* could be due to having a single available model in those areas, *C. lepidus.* In recent years Val Verde County, Texas, has had increased rainfall, and the *blairi* form, first collected in 1948

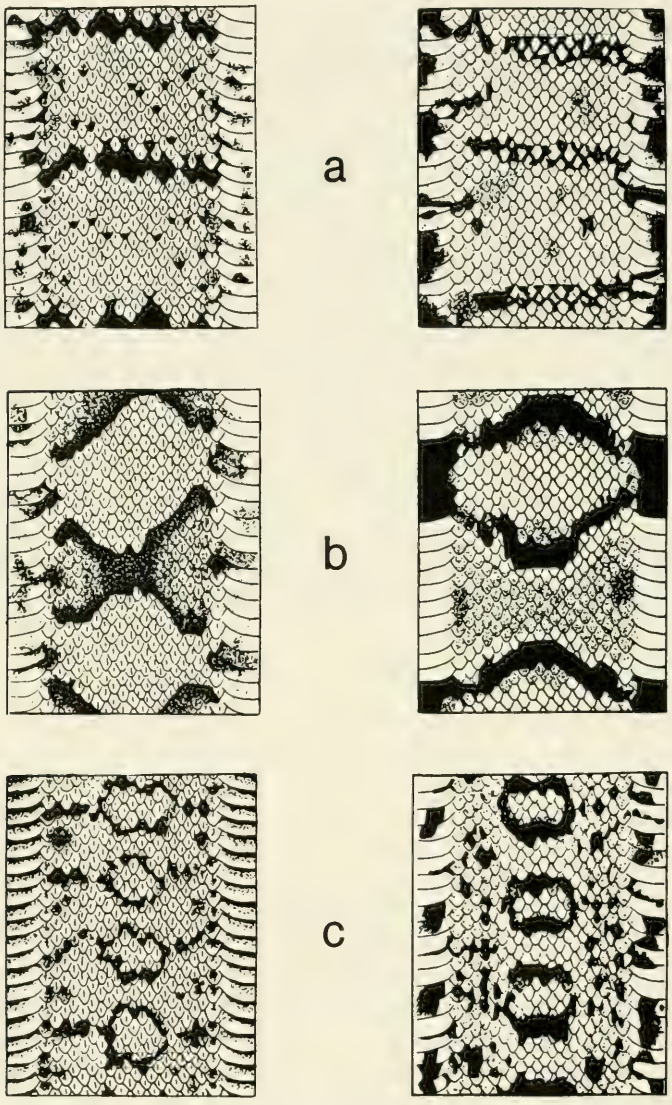


Figure 8. Hypothesis of mimicry in the *mexicana* group. a) *Crotalus lepidus* (L) with sympatric *L. alterna* (R); b) *Agkistrodon mokeson* (L) with sympatric *blairi* morph of *L. alterna* (R); and c) *Crotalus triseriatus* (L) with sympatric *L. mexicana* (R).

(Axtell, 1951), is today quite commonly found. *Agkistrodon* are common along the Devil's and Pecos river drainages as well, in similar habitat with *blairi; Micrurus fulvius* is found there as well. The sporadic appearance of *blairi*-like animals in Presidio and Brewster counties in the Big Bend region is correlated with the distribution of *Agkistrodon.* Both *A.m. pictigaster* and *M. fulvius* are very conspicuous, brightly colored animals, and though *C. lepidus* is also sympatric in Val Verde County, its dull appearance may make it a less efficient model. The increased red in the *blairi* morph may be a result of stimulus generalization by predators.

In San Luis Potosí *Crotalus triseriatus aquilis* shares the range and habitat of *mexicana.* The pattern match of these animals is quite remarkable. In life, *C.t. aquilis* is gray-brown with black speckling and a mid-dorsal row of 28 to 40 (mean = 34.5, Klauber, 1952) almost rectangular red-brown irregular blotches. Ventrolateral black blotches are also present. The W.W. Brown 1923 collection at Alvarez for the MCZ contained 10 *mexicana* and 20 *C.t. aquilis.*

The color variability of *mexicana* in the Nuevo León population sampled could reflect the local variability of the model, *Crotalus lepidus,* or a multiple model system. In that area *C. lepidus* varies from ochre to blue in background color, with deep reddish-orange on the ventral side of the tail, which is also apparent in *C.t. aquilis.* Some *mexicana* from Nuevo León are clearly ringed, like *Micrurus. Micrurus fulvius* is present on the Atlantic versant of the Sierra Madre. The mobility of predatory birds, as well as the relative rarity of the crotaline model, could affect the occurrence of mimicry in *mexicana.*

There are two situations in which the mimicry hypothesis is less certain. The population of *mexicana* in Durango, Mexico, is rather uniform in appearance and not clearly like any other snake found there. Possible models which share the same canyons with *mexicana* are *C. lepidus, C. pricei,* and *C. willardi.* The *mexicana* are most like male *C. lepidus* in that both are yellow-green to gray-green in background color with contrasting narrow dark crossbands. The *mexicana,* however, have many more bands and the bands are usually red-centered. The second situation concerns *ruthveni.* On the same hills in southwestern Querétaro where *ruthveni* is locally abundant, *C. triseriatus* is also abundant, yet *ruthveni* is a brightly ringed animal. *Micrurus fitzingeri* is sympatric with *ruthveni* over much of

its range, but appears not to be present at those localities. *M. fitzingeri* is ringed similarly to *ruthveni,* with up to 28 triads of more or less equal annuli (Smith and Taylor, 1966). Again, the conspicuousness of the red color may contribute to its stimulus value.

An alternate prediction can be made (Levene, 1953) that the areas showing polymorphism are in some way spatially patchy. The habitat of *mexicana* in Nuevo León could be considered patchy in that there are, in close proximity, areas of pine forest, chaparral, open desert, and natural and man-made meadows. There is, however, no correlation of observed morph to microhabitat. There is some spatial heterogeneity in *alterna* habitat also, with *alterna* found in both riparian and desert situations. However, this does not correlate with the distribution of the *blairi* and *alterna* morphs.

Parallel selection processes for crypsis in both the "model" and "mimic" could also explain the similarity of pattern in each situation. The *blairi* case, however, with the change of color pattern of *alterna* to the more abundant and conspicuous model *Agkistrodon,* even in the presence of *C. lepidus,* argues strongly for something other than parallel selection.

DESCRIPTIONS AND DIAGNOSES OF THE TAXA

Lampropeltis alterna (Brown)

Ophibolus alternus Brown 1901
Lampropeltis alterna, Stejneger and Barbour 1917
Lampropeltis blairi Flury 1950
Lampropeltis mexicana blairi, Gehlbach and Baker 1962
Lampropeltis mexicana alterna, Gehlbach and Baker 1962

Type specimen (holotype): Acad. Nat. Sci. Phil. 14977
Type locality: Davis Mountains, Jeff Davis County, Texas
Description and Diagnosis: A moderately sized (to about 1 m) snake with a very distinct head and overall mottled grey color. The pattern is a series of white-edged black blotches or saddles that may be red-centered. Alternating reduced markings may be present between major markings. The iris of the relatively large eye is silver-grey in color. The number of ventral scales is 210–232. The proximate spines on the hemipenes are ovoid in cross section and approximately 0.7 mm long.

Distribution: Specimens have been collected over the entire Mapimian portion of the Chihuahuan Desert (Morafka, 1977). These localities range from latitude 32° N (Worthington, 1974) south to latitude 25° N (Tanzer, 1970).

Lampropeltis mexicana (Garman)
Ophibolus triangulus var. *mexicanus* Garman 1884
Oreophis boulengeri Duges 1897
Coronella mexicana, Gunther 1900
Coronella leonis Gunther 1900
Lampropeltis mexicana, Blanchard 1921
Lampropeltis leonis, Blanchard 1921
Lampropeltis leonis, Loveridge 1924
Lampropeltis thayeri Loveridge 1924
Lampropeltis greeri Webb 1961
Lampropeltis mexicana greeri, Gehlbach and Baker 1962
Lampropeltis mexicana thayeri, Gehlbach and Baker 1962
Lampropeltis mexicana mexicana, Gehlbach and Baker 1962

Type specimen (syntypes): MCZ 4652, 4653
Type locality: near Ciudad San Luis Potosí, Mexico
Description and Diagnosis: A moderately sized (to about 1 m) snake with a slightly distinct head and overall mottled grey to yellow or brown color. The pattern is a series of white-edged black blotches, saddles or rings that may be red-centered. Alternating reduced markings may be present, usually ventrolaterally, between major markings. The anterior tail blotch is enlarged ventrolaterally and red extends onto or usually across the subcaudals. The iris of the relatively large eye is yellow-brown in color. The number of ventral scales falls between 190 and 212. The proximate spines of the hemipenes are rhomboidal in cross section and are approximately 0.4 mm long.
Distribution: Specimens have been collected mainly from the mountains surrounding the Saladan portion of the Chihuahuan Desert (Morafka, 1977). The localities have ranged from about latitude 25° N in the Sierra Madre Oriental (P. Bartlett, personal communication) south to 21° N (Duges 1897). A single desert locality (D. Morafka, personal communication) may be a result of recent man-altered changes in the habitat.

Lampropeltis ruthveni Blanchard

Lampropeltis ruthveni Blanchard 1921

Lampropeltis triangulum arcifera, Williams 1978 (in part)

Type specimen (holotype): USNM 46558

Type locality: Potrenaro = Patzcuaro?, Michoacán, Mexico

Description and Diagnosis: A moderately sized (to about 0.8 m) snake with a slightly distinct black head and a uniformly ringed pattern. The black rings are light-edged and red-centered and extend entirely around the body. The small amount of background color is a mottled tan to lime green. The iris is yellow-brown in color. The number of ventral scales falls betwen 182 and 196.

L. ruthveni can be distinguished from the central Mexican milk snakes *L.t. nelsoni* and *L.t. arcifera* on several features of external morphology. First, the head of *L. ruthveni* is distinct from the neck, as in *L. mexicana.* Second, the ringed pattern of *L. ruthveni* is uniform; the red is not much broader nor is the background color much narrower than the black as in *L.t. nelsoni.* Third, there is no tendency in any of the *L. ruthveni* examined for the black to extend along the dorsal midline through the red, as is the case in both *L.t. nelsoni* and *L.t. arcifera* (Smith, 1942; Williams, 1978). Fourth, the black rings of *L. ruthveni* are bordered with a lighter color, usually a pale lime green; this is similar to *L. mexicana* and is distinct from *L. triangulum.* Finally, the ventral scales of the *L. ruthveni* examined were never greater than 196 (mean = 188), while the range of ventrals of *L.t. nelsoni* is 203–231 and of *L.t. arcifera* is 197–217.

Distribution: The type locality is cited (Blanchard, 1921) as Pátzcuaro, Michoacán, but this may be incorrect. The locality with the specimen is Potrenaro, Michoacán. The base camp of the collector, W.E. Nelson, in August 1892 was Pátzcuaro (F. McCullough, personal communication). Recent collections have been in the vicinity of La Piedad, Querétaro (C. Lieb, J. Dixon, E. Wagner, personal communication and personal observation), Morelia (UMSNH) and Contepec, Michoacán (D. Armstrong and J. Campbell, personal communication) and Tapalpa, Jalisco. All of the recent collections have been in rocky, wooded uplands. The range of this species may extend entirely across the Mexican Plateau.

SPECIMENS EXAMINED

Lampropeltis alterna. MEXICO: *Coahuila:* Cuatrociénegas (FMNH 47090); Cruz Verde Mt. c. Saltillo (USNM 110819); Puente de la Muralla c. Monclova (Garstka coll., 1 spec.). *Durango:* 26 mi. N San Juan del Río (TCWC 36892). UNITED STATES, TEXAS: *Brewster Co.:* hills N of Study Butte (MCZ 157763). *Jeff Davis Co.:* 17.7 mi. N Fort Davis (TCWC 26181). *Presidio Co.:* 25 mi. W Lajitas (UTA 7875). *Val Verde Co.:* W of Comstock (UTA 2633); 8 mi. W of Comstock (UTA 2941); 8.5 mi. N of Comstock (UTA 8690); 32 mi. NW of Comstock (TCWC 33759); 2 mi. W of Comstock (TCWC 30515); N of Comstock (MCZ 157764, 157765; Garstka coll., 1 spec.); 15 mi. NE Del Río (TCWC 26179); 1.5 mi. E of Langtry (UTA 6680); 7.5 mi. E of Langtry (UTA 6681); N of Langtry (UTA 7188); 6 mi. N of Langtry (UTA 8671); Langtry Loop Road (MCZ 156175); 1 mi. E of Langtry (Garstka coll., 1 spec.); 11 mi. N of Loma Alta (UTA 8668); c. 10 mi. S of Loma Alta (UTA 7874); 0.5 mi. E of Pecos River on US 90 (UTA 8095); Roadside rest c. Pecos River (UTA 8568); Pecos River overlook (TCWC 26180). NO SPECIFIC LOCALITY: (UTA 7969, 8179); (Wagner coll., no. 19). CAPTIVE-HATCHED: Gravid female collected 8.7 mi. N of Comstock (TCWC 33761–33763). CAPTIVE-BRED: *Male parent* collected Brewster Co., Christmas Mts.; *Female parent* collected Val Verde Co., c. Langtry (MCZ 156271–156273); *Both parents* collected Val Verde Co., c. Langtry (MCZ 157724–157728; 156173, 156174; Garstka coll., 10 spec.); *Both parents* collected no specific locality (Texas) (MCZ 156259–156270, 157755–157758, 157760–157762, 158326–158335; Garstka coll., 1 spec., UTA 8126–8129, 7873; Wagner coll., 1, 5, 7, 19, 21–25, 34, 44).

Lampropeltis mexicana. MEXICO: *Durango:* 42 mi. S of Cd. Dgo. (UCM 21061); 23 mi. S of Cd. Dgo. (Wagner coll., G1, G2); Canyon of the Río Tunal (Garstka coll., 2 spec.); Highway 40 at the Río Chico (LACM 107230, 107231); Rancho Sta. Barbara (Houston Zoo, 1 spec.); no specific locality (San Diego Zoo, 9 spec.). *Nuevo Léon:* c. Galeana, Linares-San Roberto highway (ITESM 2507, 2508); Galeana (TCWC 56823); 5 mi. SE of Galeana (TU 16483); c. Los Lirios (ITESM uncataloged); Ojo de Agua c. Galeana (FMNH 30819–30821); c. La Angostura (Garstka coll., 3 spec.); no specific locality (BMNH 146–1–4–10). *San Luis Potosí:* Alvarez

(MCZ 19022–19025, 24976–24979; AMNH 77602; USNM 120823); c. Armadillo de los Infantes (Wagner coll., 1 spec.); c. Rioverde (KU 85010); c. Cd. San Luis Potosí (MCZ 4652, 4653); 52 mi. WNW of Cd. San Luis Potosí (CM 59980). *Tamaulipas:* Miquihuana (MCZ 19551). CAPTIVE-BRED: *Both parents* collected Mexico, Durango, no specific locality (MCZ 157754; Garstka coll., 1 spec.; Wagner coll., G3, G5). *Both parents* collected Mexico, Nuevo León, c. La Angostura (MCZ 156274–156277, 157766; also Garstka coll.)

Lampropeltis ruthveni. MEXICO: *Michoacán:* Club Campestre at Morelia (UMSNH uncataloged); Potrenaro = Patzcuaro? (USNM 46558). *Querétaro:* Canyon of the Río Galindo c. Amealco (MCZ 161010–161012; Mexican govt. coll., Agencia Forestal y de la Fauna Z–06586, Z–06587; Garstka coll., 5 spec.; Wagner coll., 9 spec.; 5 spec. released at site of capture). *Jalisco:* Mts. W Zacoalco (KU 155528); Tapalpa (SDMNH 46093); 6.5 mi. E Tapalpa (LACM 37307).

ACKNOWLEDGMENTS

I would most like to thank E. E. Williams for his patience and presence throughout this study. T. Fritts was instrumental in the early stages of the study, as were many discussions with D. F. Retes, E. Wagner, and others. G. C. Mayer criticized several drafts. D. Crews, J. Dixon, M. Scott, and two reviewers also commented on the manuscript. Access to specimens was provided by: J. Alvarado, Universidad Michoacana de San Nicolas Hidalgo, Morelia, Michoacán, Mexico (UMSNH); P. Bartlett, Instituto Tecnológico y Escuela Superior de Monterrey, Monterrey, Nuevo León, Mexico (ITESM); R. Bezy & J. Wright, Los Angeles County Museum (LACM); J. Dixon, Texas Cooperative Wildlife Collection (TCWC); W. Duellman, University of Kansas (KU); H. Dundee, Tulane University (TU); T. Fritts, San Diego Museum of Natural History (SDMNH); A. G. C. Grandison, British Museum (Natural History) (BMNH); W. R. Heyer, United States National Museum (USNM); D. Hoffmeister, University of Illinois Museum of Natural History (UIMNH); P. Maslin, University of Colorado Museum (UCM); C. J. McCoy, Carnegie Museum (CM); W. Pyburn, University of Texas at Arlington (UTA); T. Van Devender, University of Arizona (UA); and R. Zweifel, American Museum of Natural History (AMNH). Access to specimens was also provided by numerous zoo

and private collections, especially J. Bacon (Zool. Soc. San Diego), J. Murphy (Zool. Soc. Dallas), H. Quinn, and B. Tryon (Zool. Soc. Houston), E. Wagner (Zool. Soc. Seattle) and D. F. Retes. Botanical material was identified by J. Henrickson, T. Wendt, and M. Donaghue.

Permission to collect in Mexico was issued by Lic. M. L. Cossio-Gabucio, Lic. I. Ibarrola-Bejar, and Lic. M. Gonzalez-Escamilla, all of the Agencia Forestal y de la Fauna.

LITERATURE CITED

AUFFENBERG, W. 1955. A reconsideration of the racer, *Coluber constrictor*, in the eastern United States. Tulane Stud. Zool., **2**(6): 89–155.

_____. 1963. The fossil snakes of Florida. Tulane Std. Zool., **10**(3): 132–216.

AXTELL, R. W. 1951. An additional specimen of *Lampropeltis blairi* from Texas. Copeia, **1951**(4): 313–314.

BAKER, R. S., G. A. MENGDEN, AND J. J. BULL. 1972. Karyotypic studies of thirty-eight species of North American snakes. Copeia, **1972**(2): 257–265.

BLANCHARD, F. N. 1920. A synopsis of the kingsnakes: genus *Lampropeltis* Fitzinger. Occas. Pap. Mus. Zool. U. Mich. No. 87, pp. 1–8.

_____. 1921. A revision of the kingsnakes, genus *Lampropeltis*. Bull. U.S. Nat. Mus. No. 114, vi + 260 pp.

BRATTSTROM, B. H. 1955. The coral snake mimic problem and protective coloration. Evolution, **9**(2): 217–219.

BROWN, A. E. 1901. A new species of *Ophibolus* from western Texas. Proc. Acad. Nat. Sci. Phil., **53**(3): 612–613.

BULLOCK, R. E., AND W. W. TANNER. 1966. A comparative osteological study of two species of colubridae (*Pituophis* and *Thamnophis*). BYU Sci. Bull., **8**(3): 1–29.

BURY, R. B., F. GRESS, AND G. C. GORMAN. 1970. Karyotypic survey of some colubrid snakes from western North America. Herpetologica, **26**(4): 461–466.

CAMIN, J. H., AND P. R. EHRLICH. 1958. Natural selection in water snakes (*Natrix sipedon* L.) on islands in Lake Erie. Evolution, **12**(4): 504–511.

COPE, E. D. 1898. The crocodilians, lizards and snakes of North America. Ann. Rep. USNM, **1898:** 153–1270.

DOWLING, H. G. 1951. A proposed standard system of counting ventrals in snakes. Brit. J. Herpetol, **1**(5): 97–98.

DUGES, A. 1897. Description d'un ophidien noveau de Mexique, *Oreophis boulengeri* (g. et sp. nn.) Proc. Zool. Soc. Lond., **1897:** 284–285.

ECHTERNACHT, A. C. 1973. The color pattern of *Sonora michoacensis* (Duges) (Serpentes, Colubridae) and its bearing on the origin of the species. Breviora Mus. Comp. Zool. No. 410, pp. 1–18.

FLURY, A. 1950. A new kingsnake from trans-Pecos Texas. Copeia, **1950**(3): 215–217.

Fox, W., G. Gordon, and M. H. Fox. 1961. Morphological effects of low temperature during the embryonic development of the garter snake, *Thamnophis elegans*. Zoologica, **46**(5): 57–71.

Gans, C. 1961. Mimicry in procryptically colored snakes of the genus *Dasypeltis*. Evolution, **15**(1): 72–91.

Garman, S. 1884. The reptiles and batracians of North America, part 1. Ophidia. Memoirs Mus. Comp. Zool., **8**(3): xxxi + 185.

Gehlbach, F. R. 1967. *Lampropeltis mexicana* (Garman) pp. 55.1–55.2. *In* H. G. Dowling (ed.), Catalogue of American Amphibians and Reptiles. Soc. Study of Amphib. Rept.

———. 1972. Coral snake mimicry reconsidered: the strategy of self-mimicry. Forma et Functio, **5**(4): 311–320.

Gehlbach, F. R., and J. Baker. 1962. Kingsnakes allied with *Lampropeltis mexicana:* taxonomy and natural history. Copeia, **1962**(2): 291–300.

Gehlbach, F. R., and C. McCoy. 1965. Additional observations on variation and distribution of the gray-banded kingsnake, *L. mexicana* (Garman). Herpetologica, **21**(1): 35–38.

Goodman, J.D., and J. M. Goodman. 1976. Contrasting color and pattern as enticement display in snakes. Herpetologica, **32**(2): 145–148.

Greene, H. W., and W. F. Pyburn. 1973. Comments on aposematism and mimicry among coral snakes. Biologist, **55**(4): 144–148.

Gunther, A. 1900. Biologia Centrali-Americana: Reptilia and Batrachia. London, Bernard Quaritch.

Hecht, M. K., and D. Marien. 1956. The coral snake mimic problem: a reinterpretation. J. Morphol., **98**(2): 335–365.

Jackson, J. F., W. Ingram, and H. W. Campbell, 1976. The dorsal pigmentation pattern of snakes as an antipredator strategy: a multivariate approach. Am. Nat., **110:** 1029–1953.

Jameson, D. L., and A. G. Flury. 1949. The reptiles and amphibians of the Sierra Vieja range of southwestern Texas. Texas J. Sci., **1**(2): 54–79.

Johnson, R. G. 1955a. The application of X-rays to the study of small reptiles and amphibians. Copeia, **1955**(3): 259–261.

———. 1955b. The adaptive and phylogenetic significance of vertebral form in snakes. Evolution, **9**(4): 367–388.

Klauber, L. 1941. The correlation between scalation and life zones in San Diego County snakes. Bull. Zool. Soc. San Diego No. 17, pp. 73–79.

———. 1952. Taxonomic studies of the rattlesnakes of mainland Mexico. Bull. Zool. Soc. San Diego No. 26, pp. 1–143.

Laszlo, J. 1975. Probing as a practical method of sex recognition in snakes. Int. Zoo Year Book, **15:** 178–179.

Levene, H. 1953. Genetic equilibrium when more than one ecological niche is available. Am. Nat., **87:** 311–313.

Loveridge, A. 1924. A new snake of the genus *Lampropeltis*. Occas. Pap. Boston Soc. Nat. Hist., **5:** 137–139.

Mecham, J., and W. Milstead. 1949. *Lampropeltis alterna* from Pecos County, Texas. Herpetologica, **5**(6):140.

MILLER, D. J. 1979. A life history study of the gray-banded kingsnake, *Lampropeltis mexicana alterna* in Texas. Chihuahuan Desert Research Institute, Contrib. No. 87, pp. 1–48.

MINTON, S. A. 1976. Serological relationships among some congeneric North American and Eurasian colubrid snakes. Copeia, **1976**(4): 672–678.

MINTON, S. A., AND S. K. SALANITRO. 1972. Serological relationships among some colubrid snakes. Copeia, **1972** (2): 246–252.

MORAFKA, D. 1977. A biogeographical analysis of the Chihuahuan Desert through its herpetofauna. Biogeographica vol. 9. The Hague, Junk, vi + 313 pp.

MURRAY, L. J. 1939. Annotated list of amphibians and reptiles from the Chisos Mountains. Contrib. Baylor Mus., **24:** 4–16.

PETERS, J. 1964. Dictionary of Herpetology. N.Y., Hafner, vii + 427 pp.

POUGH, F. H. 1976. Multiple cryptic effects of crossbanded and ringed patterns of snakes. Copeia, **1976**(4): 834–836.

SMITH, H. M. 1941. *Lampropeltis alterna* from Mexico. Copeia, **1941**(2): 112.

_____. 1942. Remarks on the Mexican kingsnakes of the *triangulum* group. Proc. Roch. Acad. Sci., 8: 196–207.

_____. 1944. Snakes of the Hoogstraal expeditions to Northern Mexico. Field Mus. Nat. Hist. Ser. Zool., **29:** 135–152.

SMITH, H. M., AND E. H. TAYLOR. 1966. The Herpetology of Mexico. Ashton, MD., Lundberg, 610 pp.

SMITH, N. G. 1969. Avian predation of coral snakes. Copeia, **1969**(2): 402–404.

SMITH, S. M. 1975. Innate recognition of coral snake pattern by a possible avian predator. Science, **187**(4178): 759–760.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman, xxi + 776 pp.

STEJNEGER, L., AND T. BARBOUR. 1917. A checklist of North American Amphibians and Reptiles. Harvard, Cambridge, Ma.

TANNER, W. W. 1953. A study of the taxonomy and phylogeny of *Lampropeltis pyromelana* (Cope). Great Basin Nat., **13**(1,2): 47–66.

TANZER, E. 1970. Polymorphism in the *mexicana* complex of kingsnakes with notes on their natural history. Herpetologica, **26**(4): 419–428.

TAYLOR, E. H. 1940. A new *Lampropeltis* from western Mexico. Copeia **1940**(4): 253–255.

UNDERWOOD, G. 1967. A contribution to the classification of snakes. BMNH Pub. 654, x + 179 pp.

WEBB, R. 1961. A new kingsnake from Mexico with remarks on the *mexicana* group of the genus *Lampropeltis*. Copeia, **1961**(3): 326–333.

WILLIAMS, K. 1978. Systematics and natural history of the American milk snake *Lampropeltis triangulum*. Pub. Biol. Geol. Milwaukee Pub. Mus. No. 2, 258 pp.

WORTHINGTON, R. D. 1974. Western records of the Davis Mountain kingsnake, *L.m. alterna* in Texas. SW Nat., **19**(3): 330–331.

MAR 1 8 1985
HARVARD
UNIVERSITY

BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 30 JUNE 1982 NUMBER 467

THREE NEW SPECIES OF THE *ANOLIS PUNCTATUS* COMPLEX FROM AMAZONIAN AND INTER-ANDEAN COLOMBIA, WITH COMMENTS ON THE EASTERN MEMBERS OF THE *PUNCTATUS* SPECIES GROUP

ERNEST E. WILLIAMS[1]

ABSTRACT. New species of the *Anolis punctatus* group are described from central and eastern Colombia: *A. vaupesianus* from Comisaría of Vaupés, *A. huilae* from the Departments of Huila and Tolima, *A. santamartae* from the south slope of the Sierra Nevada de Santa Marta. The characters useful in discriminating the eastern members of the *Anolis punctatus* species group are discussed and evaluated, and the species themselves are diagnosed.

INTRODUCTION

Important new collections from Colombia have yielded *Anolis* that require description. Those dealt with here are allied to *Anolis punctatus* of Amazonia and the Atlantic Forest of Brazil, and, like the other recently described members of the *punctatus* group (Williams, 1965, 1974), they occur in areas peripheral to the range of that central and widely dispersed species. The three new taxa thus fill in blank areas in the known range of the complex. However, like many others of the *punctatus* species group, excepting only the central widespread and best-known species *punctatus,* these are species almost without distributions or ecologies. There are so few localities from which they are known, so little is known about their biology, that they are question marks rather than known components of fauna. They testify primarily to our basic ignorance of South American lizards.

[1]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

I first describe the Amazonian taxa. Since the three best specimens are from the Comisaría of Vaupés, I call it:

Anolis vaupesianus, new species
(Figs. 1–5 and Map)

Type: MCZ 156309 (formerly UTA 3626), adult male.

Type locality: Timbo, a Cubeo village ca. 1 N 70 W on the Río Vaupés, E of Mitú, Vaupés, Colombia, William F. Pyburn coll., 24 July 1972.

Paratypes: COLOMBIA: **Vaupés.** UTA 6850, MCZ 154592 (formerly UTA 5051)[1] same locality as type. J. K. Salser, Jr. coll.; ICN 4542, Cano Ti near Pamopeta, W. W. Lamar coll.; UTA 10283, Wacara, Lois Lores and Marilyn Cathcart coll. *Amazonas.* MCZ 79655, lower Río Apaporis, I. Cabrera coll.; MCZ 112098, Tio Miriti-Parana, La Providencia, F. Medem coll.

Description (paratype variation in parentheses). *Head:* Head scales moderately sized, weakly (sharply) keeled toward tip of snout, smooth posteriorly. Ten (8–11) scales across snout between second canthals. Frontal depression distinct, scales within it smaller than those anterior to it (not or not conspicuously so). Eleven (9–10) scales border rostral posteriorly. Anterior nasal scale divided (not divided), it and inferior nasal scale in contact with rostral. Eight (6–7) scales between supranasals. Rostral area swollen, protuberant, rostral extending well beyond mental on male (not swollen or protuberant, rostral not extending much beyond mental in female).

Supraorbital semicircles separated by one minute scale (or by one or two larger scales or narrowly in contact), separated from the supraocular disk by one row of granules. Supraocular disk ill-defined (better-defined), grading into surrounding granular scales. One elongate supraciliary followed by minute granules. Canthus distinct, five (5–6) canthal scales, the second largest. Six (5–7) loreal rows counting down from the second canthal, the ventralmost largest.

Temporals and supratemporals granular, the latter grading into larger scales around the interparietal. An ill-defined and tapering double intertemporal row of somewhat enlarged scales. Inter-

[1]This is a specimen referred to as *A. punctatus* by Greene (1977).

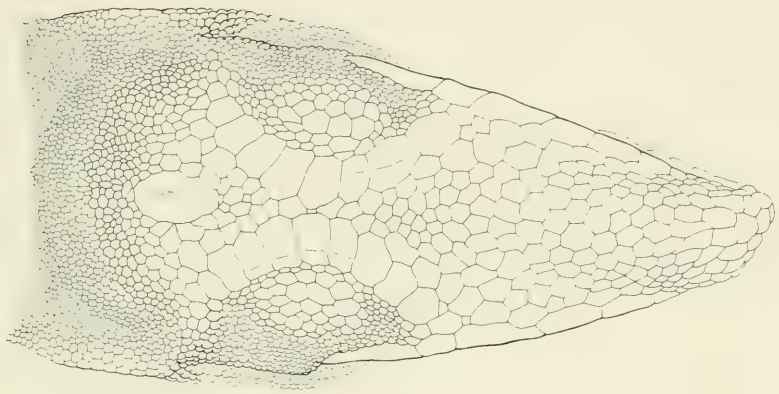


Figure 1. *Anolis vaupesianus*, n. sp. Type ♂, MCZ 156309. Dorsal view of head.

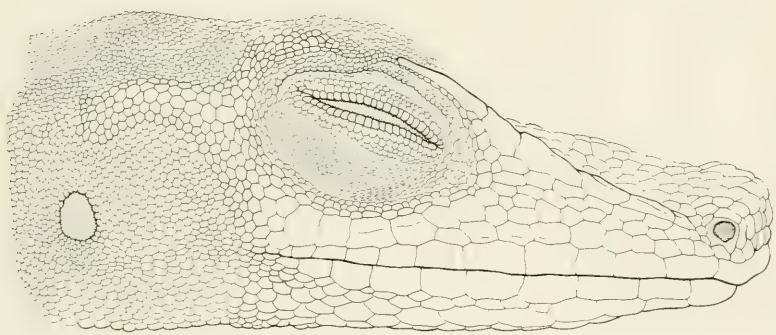


Figure 2. *Anolis vaupesianus*, n. sp. Type ♂, MCZ 156309. Lateral view of head.

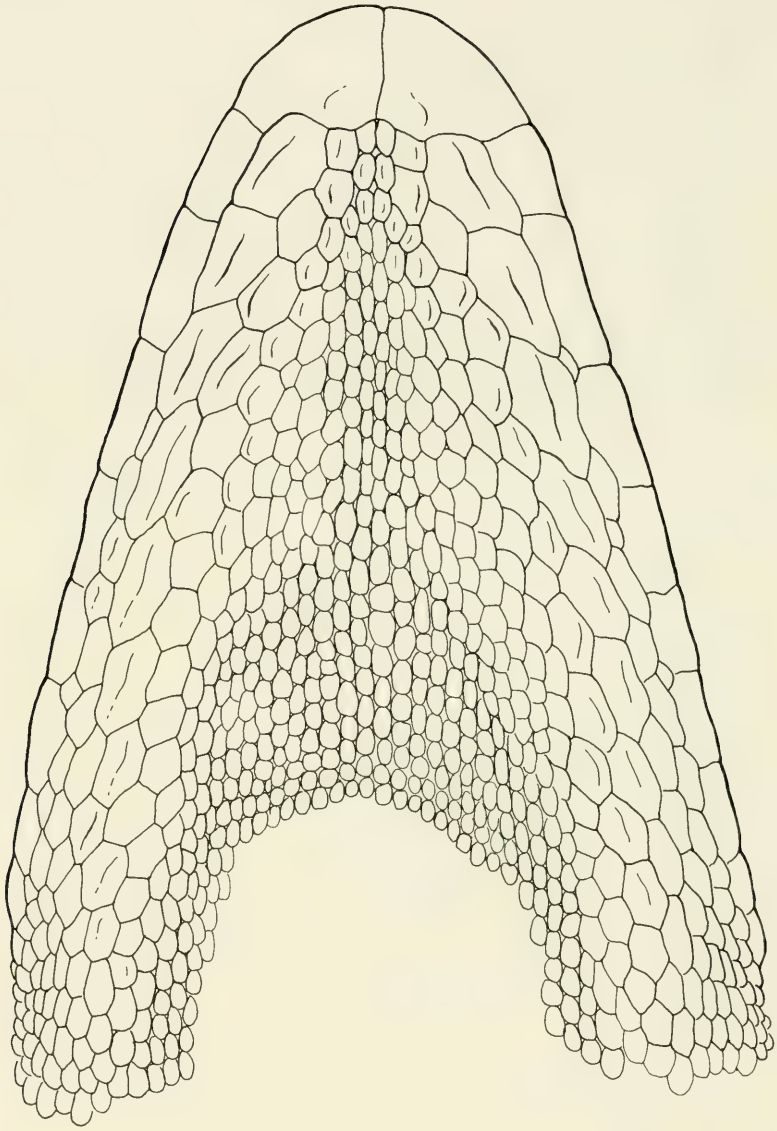


Figure 3. *Anolis vaupesianus*, n. sp. Type ♂, MCZ 156309. Ventral view of head.

Figure 4. *Anolis vaupesianus*, n. sp. Type ♂, MCZ 156309. Lateral view of whole animal.

Figure 5. *Anolis vaupesianus*, n. sp. Paratype ♀, MCZ 112098. Lateral view of whole animal.

parietal much larger than ear (larger), separated from the supraorbital semicircles by two (3) rather large scales. Scales surrounding interparietal largest anterolaterally, posteriorly grading through an area of minute scales into the dorsals that are as large as the temporals.

Suboculars weakly keeled, in contact with supralabials. Seven to eight (7–9) supralabials to center of eye.

Mental semidivided, each half distinctly wider than long, in contact with four scales between the keeled sublabials. Three (5) sublabials in contact with infralabials. Gulars small, smooth, increasing in size laterally.

Trunk: Dorsals granular, subequal, smaller than the weakly keeled ventrals which are subimbricate (juxtaposed), in transverse rows.

Dewlap: Moderate in male, not extending posteriorly much beyond axilla. Lateral scales elongate, larger than ventrals, in close-packed rows. Edge scales shorter, crowded, subimbricate. Vestigial in female.

Limbs: Largest scales on forelimb unicarinate, on digits weakly multicarinate. On hind limbs scales in front of thigh and lower leg weakly unicarinate, on back of thigh and lower leg granular. Supradigital scales weakly multicarinate. Twenty-five (22–26) lamellae under phalanges ii and iii of fourth toe.

Tail: Weakly compressed. No dorsal crest. No verticils. Scales above weakly carinate. A double middorsal row. Scales behind vent at most very weakly carinate, becoming distinctly so posteriorly. Postanal scales not well defined in male, absent in female.

Size: Male type: 82 mm snout to vent; largest male paratype: 78 mm snout to vent. Female paratype: 75 mm snout to vent.

Field notes and color in life: F. Pyburn presents the following notes on the male holotype: "24 July 1972 I collected a dark green anole on the base of a small tree in village (Timbo) about one hour before dark. Dorsum of head, body, legs dull uniform green with scattered blue flecks; venter grey; dewlap skin black; scales of dewlap grey. Lizard turns dull brown when handled. Has fleshy keel on nape and along back."

For MCZ 154592, a male, the notes below are abridged from those of J. K. Salser, Jr.: "*Anolis* sp.; Timbo (Vaupés), Colombia; March 20, 1974: very hot noon-time; caught in an aged avocado tree

- scaled tree and jumped from its top in attempt to escape... Blue dots dorsolaterally placed in stripes from vertebra down, angling down to lower sides; changes from dark green to green-brown mottled very quickly; eyes golden, eyelid border yellow..."

For the female paratype, MCZ 112098 (Fig. 5), from the Río Miriti-Parana, Federico Medem has provided the following information: "Caught 8:30 a.m. on underbrush, one meter high, in open country... Gular sack small, greenish. Iris golden. Intense green on body with lateral small blue spots. Middorsally 16 squarish sand-colored spots. Dark transverse bars on tail. Venter light gray with dark vermiculations."

For MCZ 79655, a male, Medem reports the color as: "Dorsally green with lateral blue spots; dewlap 'morado' - violet, mulberry-colored."

Comparisons: Very few specimens of *A. punctatus* are recorded from Colombia. The nearest to any of the type series of *A. vaupesianus* are two recently collected specimens in the Paris Museum (MHNP-1978-3086-87) from Hameau Kuira, Río Agara Parana, a tributary of the Río Putumayo, in Amazonas Territory. Both are males with strongly keeled ventrals, dorsum an unpatterned dark purplish and dewlap with light skin with minute dispersed melanophores and purplish scales.

The *A. vaupesianus* most nearly adjacent to these is MCZ 79655 from La Providencia, Río Miriti-Parana, a tributary of the Río Caquetá, also in Amazonas. It is unfortunately a female. MHNP-1978-3086 has therefore been compared with the topotypic paratype UTA 6850, which is of the same size and sex. The dewlap in the paratype contrasts strongly with the Amazonas *punctatus* in its intensely black skin and white scales, and the ventral scales in *vaupesianus* are smaller and decidedly more weakly keeled. No other scale differences are evident, but the color and pattern of the Mitu paratype as preserved are strikingly different from anything observed in *punctatus:* it is brown, strongly blotched with darker, the dorsal blotches tending to form transverse series across the back. Anteriorly, a dark V, the apex backward, formed of somewhat irregular blotches, reaches the middle of the orbit on each side. A less well defined V in medial to this, reaching to the tops of the orbits.

This very distinctive color and pattern are not, however, seen in the remainder of the type series of *vaupesianus* which, as preserved,

are not strikingly dissimilar to *A. punctatus.* At best the distinctive pattern of UTA 6850 represents an element of the pattern repertoire of *A. vaupesianus* not present in *A. punctatus.* It clearly will not serve to distinguish most specimens.

Habitat: The few notes on *vaupesianus* available give little indication of its ecology, except that it is associated with trees. The fact that the type was caught in a village probably indicates that it is an edge animal, not characteristic of the dark forest.

The second species was first discovered in the Departamento del Huila. It has therefore been called:

Anolis huilae, new species
(Figs. 6–9 and Map)

Type: ICN 3725, an adult male, collected by Helen Chin, October, 1976.

Type locality: Herberto Herrera's coffee plantation, Palestina, Huila, Colombia.

Paratypes: COLOMBIA: **Huila.** KU 169830-31, Parque Arqueológico San Agustín, 3 km SW San Agustín, 1750 m; ICN 3726, MCZ 159121-22: Palestina; MCZ 156305: Quebrada La Cascajosa, Parque Nacional Natural La Cueva de los Guácharos (northern boundary); INDERENA R-0297, -0562, -0665, MCZ 156306, 156316: Parque Nacional Natural La Cueva de los Guácharos; ICN 4461-62: 62 km (by road) NW San Isidro de Isnos, 1940 m. **Tolima.** ICN 3732: Amaine; ICN 3727-31, 3733, INDERENA (numbers not now available, formerly UVMP 4400, 4404), MCZ 159112-117: Cajamarca; Cali (Univ. Valle, Depto. Biol.) UVC 38, 191, ICN 3735-36, MCZ 159119-120: Juntas; ICN 3734, MCZ 159118: Llanitas, 10 km N Ibagué.

[Referred specimen: Meta: ICN 4541 ca. 3–4 km NNE of Manzanares.]

Description (paratype variation in parentheses). *Head:* Most head scales smooth, slightly concave, a few convex, obtusely keeled. Ten (8–11) scales across snout between second canthals. A few *narrow* scales in the frontal depression much smaller than surrounding scales. Eight (7–9) scales border rostral posteriorly. Anterior and inferior nasal scales in contact with rostral. Seven (6–7) scales dorsally between nasals. Snout not protuberant in male.

Supraorbital semicircles broadly in contact with each other and with the supraocular disks. Supraocular disks with few (several)

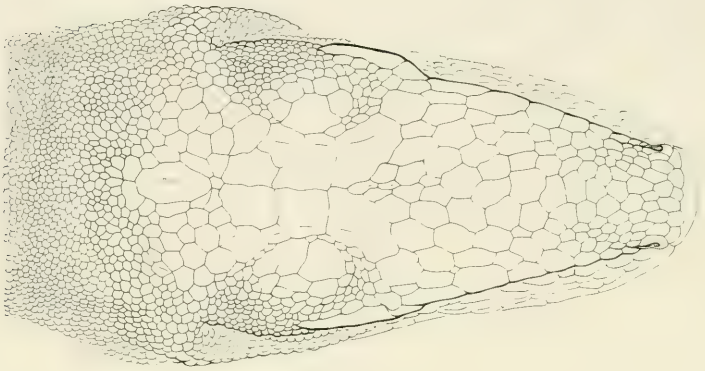


Figure 6. *Anolis huilae,* n. sp. Paratype ♂, MCZ 159015. Dorsal view of head.

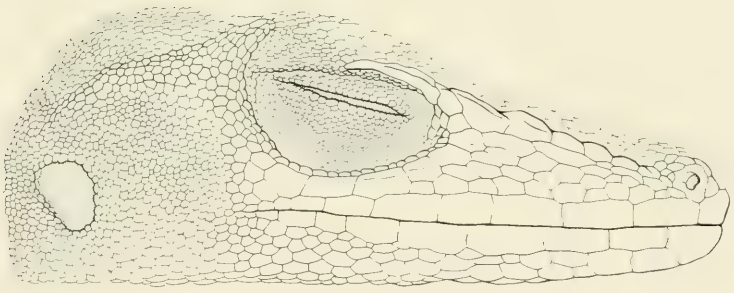


Figure 7. *Anolis huilae,* n. sp. Paratype ♂, MCZ 159015. Lateral view of head.

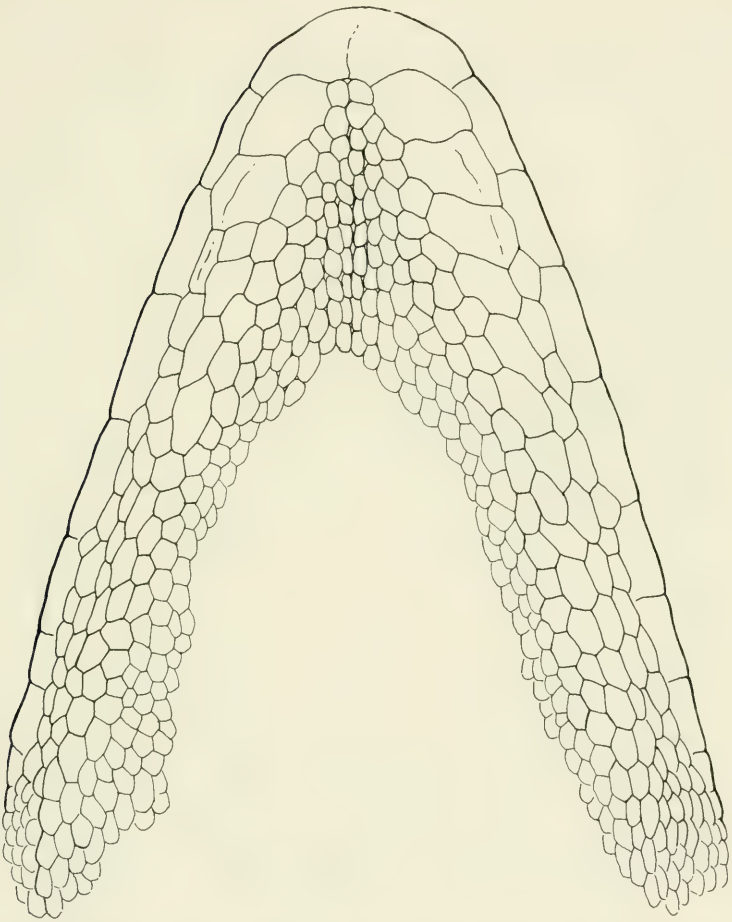


Figure 8. *Anolis huilae,* n. sp. Paratype ♂, MCZ 159015. Ventral view of head.

large smooth scales. One elongate supraciliary on each side followed by granules. Canthus blunt, ca. 8 canthal scales, the second and third largest. Five (4–5) loreal rows, counting down from the second canthal, subequal.

Temporals slightly smaller than the supratemporals, both granular. No differentiated intertemporal line of enlarged scales. The scales surrounding the interparietal abruptly larger, those anterior and lateral largest (not so in female). Interparietal equal to (smaller

Figure 9. *Anolis huilae*, n. sp. Paratype ♂, MCZ 159015. Lateral view of whole animal, dark phase.

or larger than) ear, separated from the supraorbital semicircles by 2–3 (0–2) scales. Large scales posterior to interparietal followed by minute granules on nape, distinctly smaller than the granular dorsals.

Suboculars keeled, in contact with supralabials, continued posterior to the eye by two distinct (less distinct) rows of smaller scales, anteriorly meeting canthals. Seven (5–7) supralabials to center of eye (supralabial five is much the longest in one paratype, an obvious anomaly; in the type, the supralabials are nearly subequal).

Mental semidivided, in contact with three (1–4) scales between the very large, smooth sublabials. Three sublabials (1–4) in contact with infralabials. Central throat scales small, swollen, oval, becoming abruptly longer laterally alongside the sublabials.

Trunk: a few middorsal (2–4) rows indistinctly enlarged, weakly or distinctly keeled, grading into granular flank scales. Ventrals much larger than largest dorsals, smooth, imbricate or subimbricate (juxtaposed in female), not in distinct transverse rows (in transverse rows).

Dewlap: Large in male, extending to midbelly (absent in female). Scales at edge larger than ventrals, smooth. Lateral scales smooth, in double rows separated by naked skin.

Limbs: Limb scales weakly uni- or multicarinate. Supradigital scales multicarinate. Twenty-one (22) lamellae under phalanges ii and iii of fourth toe.

Tail: Slightly compressed, without crest. Enlarged postanals present (absent in female). A double row of keeled scale middorsally on tail. Scales behind vent smooth.

Size: The male type is 75 mm in snout-vent length. The largest male reaches 82 mm.

Color in life: Helen Chin reports topotypic animals as 'parrot green' in the trees. Her color transparencies show tan and reticulate animals after capture.

Color notes are available for two MCZ specimens. MCZ 156405, a male: "Dorsum bright green with yellow spots (seven large spots along the spine). Tail banded green and black. A white dot inside a black ring on side of neck behind the ear. Eyelid yellow, iris grey. Chin grass-green. Dewlap yellow with six green stripes, these bordered by numerous black dots. Rest of underparts greyish."

MCZ 156306, a female: "Dorsum with wide tan stripe from back

of head to halfway down tail, at which point it becomes speckled with black dots. Rest of back grey-green, darker next to tan stripe, and lighter with dark patches on the sides. Legs banded black and light green. Head light green with dark around eyes. Tip of tail bronzy. Venter yellow with few small black spots."

Both these specimens are near-topotypes. Palestina is a settlement at the beginning of the 22 km trail leading to the Parque Nacional Natural La Cueva de los Guácharos.

The colors in life of the Kansas specimens from Parque Arqueológico de San Agustín are described rather differently (although not in the same detail): "At night - dorsum pale green with brown reticulations. Dewlap cream with grey-bordered white streaks. Iris creamy-grey. Tongue orange."

Notes are at hand also for two females collected by Pedro Ruiz and J. D. Lynch near San Isidro de Isnos (notes by Lynch):

ICN 4461: "Sleeping on leaf in forest near stream. Iris yellowish. Ground color dull green with brown barring; greenish cream spots on flanks; tail barred brown and medium brown with cream edges; venter dirty cream with brown spots. Throat the same but with greenish cast."

ICN 4462: "Sleeping on Ortega, 3 m above stream at edge of corn field. Iris grey brown. Tongue pale orange yellow."

Dennis M. Harris has provided notes on the series from Tolima:

"*Male:* Dorsum pale leaf-green, spotted most vividly on the sides by 1–2 mm diameter circular dots of greenish-yellow. Head slightly brownish. Eyelid yellow. Nape with a lateral spot of blue-green to black, sometimes surrounded by a yellow area, sometimes with a light center. Tail barred or not with bands equal in width to the green. Venter white to grayish. Dewlap skin pale yellow, scales cream, in rows that are edged with black spotting.

Male may change to a deep brown with vivid yellow spots. It does so when handled and possibly as a response to another male. The one brown male seen in the field was never a green one, and had a vertically flattened body and extended dewlap. (The cream scales of the dewlap may become drab greenish in the brown-phase male.)

Female: Banded or striped, light or dark brown. The stripe is crayola brown with dark brown flecks. There is no color change except for minor tone changes."

Color notes have been made available by W. W. Lamar for the single animal from Manzanares, Meta: "Dorsum dark gray with

numerous light gray-green spots. Mid-dorsum brighter than rest of the back. More green toward the center of the flanks. Tops of forelegs gray-green with lighter yellow-green elbows and feet. Hind legs with 3 light bands above knee. Three broken bands below knee. Tail pale green with 11–12 dusty bands. A black spot with an aquamarine center on the side of the neck. Yellow eye ring and snout aqua-blue-green, darker between the eyes. Venter pale yellow with dark gray spots on the sides, brighter yellow near vent, broad portion of tail, and inguinal area. A patch of aqua-blue on tail 10–25 mm from vent, rest of tail dark gray. Dewlap an overall aqua green-blue striped with pale green and dotted with black. Spaces between stripes are pale yellow. Nostril yellow. Tongue yellow."

Comparison of these notes for the Meta specimen described shortly after death with the detailed account from Huila and Tolima shows various discrepancies. Color differences in *Anolis,* however, may be described differently by different individuals or by the same person at different times. This, plus the capacity for color change, suggest caution in attributing taxonomic significance to color differences of the sort seen here. (See also comment below.) *There are no scale differences.*

Color as preserved: Most male *A. huilae* are strikingly distinctive because of the bold lateral spotting, plus the lines of dark spots on the dewlap. Some specimens display a more muted spotting. This is especially true of the individual from Manzanares, Meta. The latter seems at first distinguishable because the spotting on the dewlap is not in lines but quite random. Some specimens from Tolima, however, have the spotting on the dewlap irregular also. The Meta animal does not, on present evidence, fully match the type series; since it is also geographically peripheral (on the east side of the Andes, rather than in the Magdalena Valley) I have not made it a paratype. With only one specimen and no structural differences it is not permissible to describe it taxonomically.

Habitat: Dennis Harris reports: "found on relatively smooth bark tree *trunks* usually, between 1 and 7 meters. Males almost exclusively there, females sometimes on bushes nearby, 1 m high. Usually only single male/tree trunk (25 cm+ diameter). Shrubs seem to be only *peripheral* environments. Not found on very smooth-bark guayaba (guava) trees. Not found on trunks with heavy moss growth. Common right in town of Cajamarca and along edges of road. Males more frequently seen and more of them

caught. Only time male and female seen together on tree trunk they were copulating. Usually seen head down, out (like *frenatus*) on trunk. At Anaime *Prionodactylus argulus* found at same site. At Llanitas, 10 km from Ibagué, *Anolis antonii* and *A. huilae;* at Juntas, much higher, *Phenacosaurus* and *A. huilae*."

MCZ 156316 was found below a cave-hole of *Rupicola rupicola* among defecated seeds. Apparently a food item, it was in relatively good condition and quite recognizable.

Comparisons: A. huilae, although obviously a member of the *punctatus* species group, is not obviously closely related to any other presently described member. The color pattern of males is highly distinctive.

A third species comes from the southern slopes of the isolated Santa Marta range. It is to be called:

Anolis santamartae, new species
(Figs. 10–13 and Map)

Type: CAS 113922, adult male.

Type locality: San Sebastián de Rábago, Sierra Nevada de Santa Marta, Cesar, Colombia (10° 4″ N, 73° 16″ W), Borys Malkin coll., 1–10 April, 1968.

Paratypes: same data as type: CAS 113924, MCZ 156311.

Description (paratype variation in parentheses). *Head:* Moderately elongate. Head scales rather large, smooth, flat except for smaller bluntly keeled or swollen scales at tip of snout. Six (4–5) scales across snout between second canthals. Frontal depression distinct, the scales within it larger (some smaller) than those anterior to it. Anterior and inferior nasal scales in contact with rostral. Four (5–6) scales dorsally between supranasals. Rostral area protuberant in male, overhanging lower lip (not so in female).

Supraorbital semicircles broadly in contact with each other and with the supraocular disks. Supraocular disks well defined, comprised of 8 to 10 smooth scales. Remainder of supraocular area with large granules. Canthus distinct, four or five canthal scales, the second and third (or first and second) largest. Five (4–5) loreal rows, the lowermost largest. Temporal and supratemporal scales granular, larger at the angle of the mouth an at the angle between temporal and supratemporal regions. Scales surrounding the interparietal rather abruptly larger, largest laterally, grading into dorsals

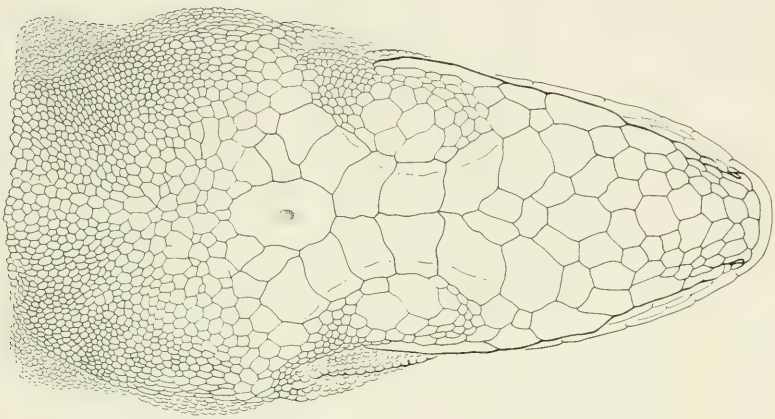


Figure 10. *Anolis santamartae*, Type ♂, CAS 113922. Dorsal view of head.

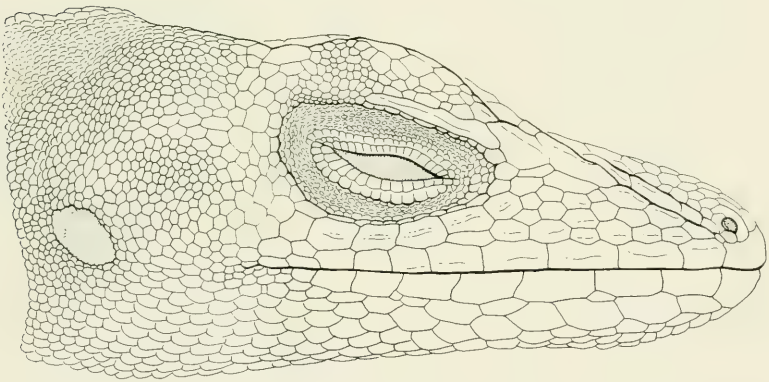


Figure 11. *Anolis santamartae*, Type ♂, CAS 113922. Lateral view of head.

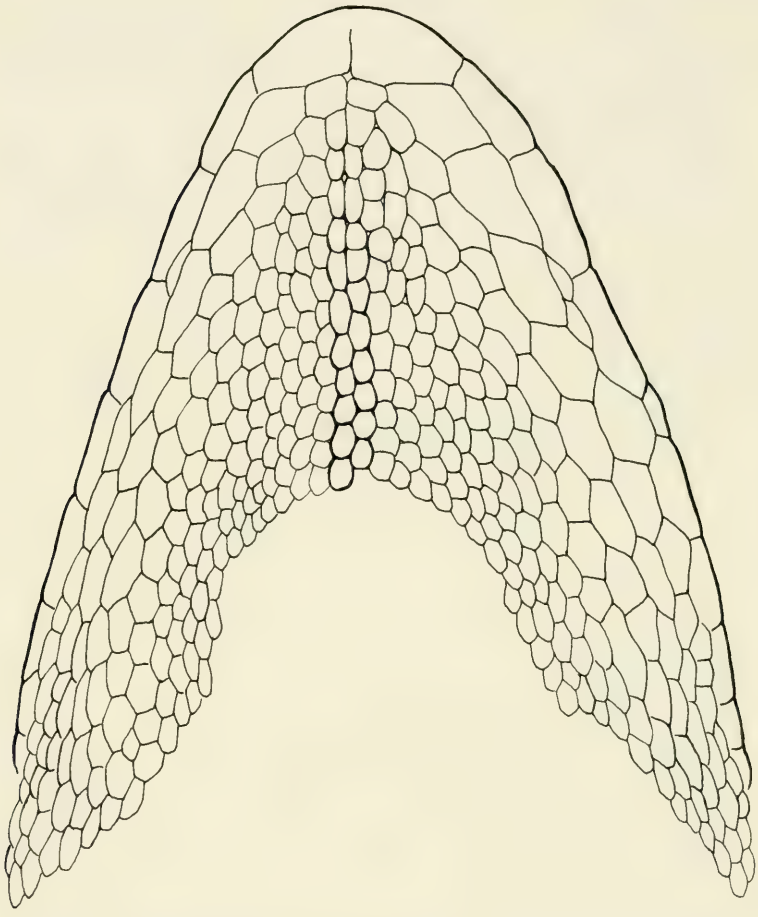


Figure 12. *Anolis santamartae,* Type ♂, CAS 113922. Ventral view of head.

posteriorly. Interparietal much larger than ear, broadly in contact with the supraorbital semicircles.

Suboculars weakly keeled, in contact with supralabials, anteriorly separated from the canthal ridge by two (1–2) scales, posteriorly grading into the temporals. Seven supralabials to the center of the eye.

Mental semidivided (mental region abnormal in MCZ 156311), in contact with two large scales between the well-developed sublabials.

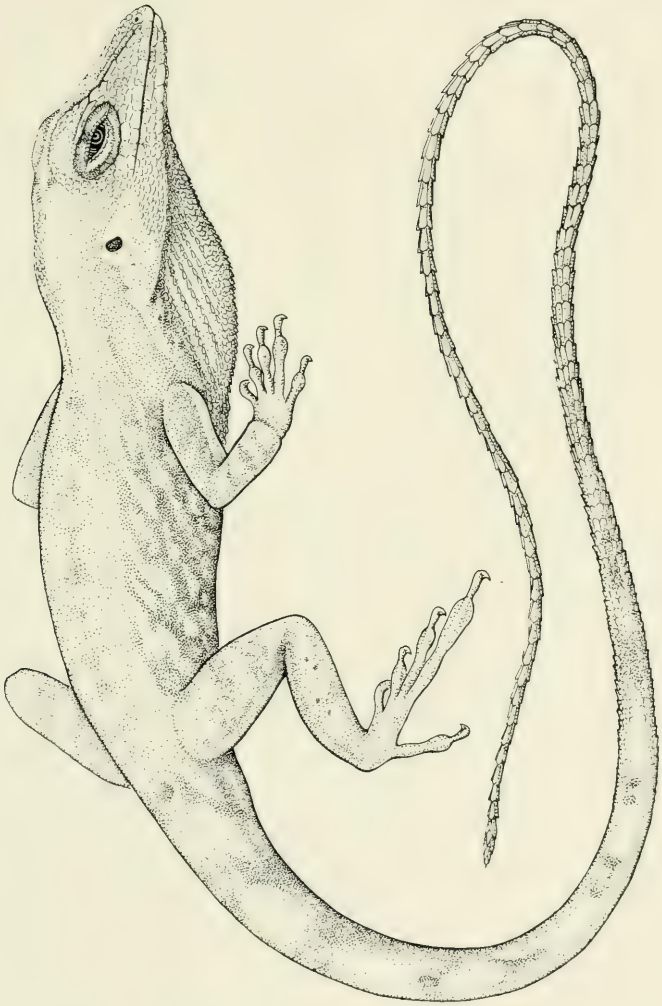


Figure 13. *Anolis santamartae, Type* ♂, CAS 113922. Lateral view of whole animal.

Figure 14. Distribution of the species described herein. ▼: *Anolis santamartae;* ○: *Anolis huilae;* and ■: *Anolis vaupesianus.*

Four (3) sublabials in contact with infralabials. Gulars rather large, swollen, increasing in size laterally and anteriorly.

Trunk: Ca. four to six middorsal rows flat, weakly keeled, subimbricate, much larger than flank granules but grading into them. Ventrals still larger, smooth or obtusely keeled. Chest scales distinctly keeled.

Dewlap: Large in male, only indicated in female. Scales in close set rows, elongate and narrow, except at edge where they are flat and smooth.

Limbs: Scales on limbs uni- to multicarinate, those on digits multicarinate. Eighteen (19–21) lamellae under phalanges ii and iii of fourth toe.

Tail: Compressed. Scales weakly to strongly carinate. A double middorsal row. No tail crest. No verticils. Scales behind vent carinate. Post-anals large (broken up on one side type, absent in female.)

Size: Male type: 50 mm, snout to vent. Male paratype: 55 mm. Female paratype: 53 mm.

Color as preserved. Female paratype: Gray-brown. A light line from suboculars to above ear. A narrow dark interorbital bar. A series of ovoid or rhomboidal dark blotches paravertebrally. Irregular oblique dark streaking on flanks. Limbs irregularly banded. Tail very weakly banded. Throat and belly smudged with darker.

Male type: Gray. A light line from suboculars to above ear. Another light line *from lower edge of ear* along lateral edge of dewlap onto underside of upper arm. Weak traces of blotching dorsally. Irregular oblique dark streaks on flanks. Limbs and tail with very weak and obscure markings. Underneath smudged with brown. Dewlap skin white, scales very light brown.

Male paratype: A dark interorbital bar. A light stripe from suboculars to above ear, another from *below* ear to shoulder. Middorsum and dorsum of tail obscurely marked with light and dark. Flanks with oblique dark streaks. Limbs smudged above. Belly with irregular dark markings. Throat with vaguer markings.

Habitat: San Sebastián is at the border between the Departments of Cesar and Magdalena, and the specimens may have been collected in either Department. The elevation is at, or above, 2,000 m. There are no ecological notes.

DISCUSSION

Comparison of *santamartae* and the other two new species of the *punctatus* complex with each other and with the other already-described members of the complex could be made in tabular form, as in Williams (1974). Here, however, I prefer to discuss and elevuate the characters on which I recognize the several species. I begin with the color differences.

Color in Life

For this purpose the few detailed descriptions of color in life of *Anolis punctatus* must be quoted.

Hoogmoed (1973) has a description for *A. punctatus 'punctatus'*[1] from Surinam: "Color in life grass-green above with sky-blue dots, eyelids purplish with a yellow rim. Chin bluish, throat greenish. Belly white to purple-green. In bright sunlight the lizards are purple with sky-blue dots. Dewlap in males yellow ochre with rows of white scales; in females the scales on the dewlap are yellow. Iris orange-brown."

A parallel description is provided by Dixon and Soini (1975) for *A. punctatus 'boulengeri'* from the Iquitos area in Peru: "The dorsal coloration of adults is leaf-green with six to seven very narrow white cross-bands confined to the upper body. The lower sides are spotted with minute white dots, and the limbs are spotted with minute dark brown spots. Occasionally specimens are deep purple dorsally, especially after being in captivity for a few hours. The white cross-bands and white spots are very distinct when the latter color prevails. Male dewlaps are orange to reddish-orange with the enlarged lateral scale rows light yellow."

P. E. Vanzolini has provided me with a translation of the unpublished field description of Helmut Sick of an *A. punctatus 'punctatus'* from the Atlantic Forest in Brazil (Río Itaunas, Espírito Santo): "General body color alive: grayish sepia, dewlap chrome yellow. Freshly killed: moss green, eyelid yellowish green, dewlap chrome yellow with stripes composed of whitish green spot, chin whitish-green. Underparts greenish-white. Digits and tail with

[1]Western specimens of *punctatus* with keeled ventrals are usually called *boulengeri* O'Shaughnessy whether as subspecies or species. See Williams and Vanzolini (1980) for evidence that 'boulengeri' is a morph and not a valid taxon.

vestiges of dark brown crossbands. Posterior two-thirds of tail grayish sepia. Flanks with lines of white spots...." Vanzolini himself describes dewlap colors for two additional specimens: (Santo Amaro dos Brotas, Sergipe): 'pure yellow'; (Lago Mapori, Rio Japura, Amazonas): 'rusty orange.'

No color descriptions from living specimens are available for *A. santamartae, A. caquetae, A. deltae,* or *A. nigropunctatus.* The color descriptions of *A. vaupesianus* and *huilae* have been given above.

There are serious problems in the comparisons of color and pattern in the members of this complex. The few good reports are for the local populations of widely scattered regions or for individual specimens. This would be a difficulty in any taxonomic group. In *Anolis* an additional problem exists: color repertoire may be extensive and tends to be especially so in the green species. In the latter, the difference between light and dark phases may be extreme, and there may be in life intermediate patterns or colors that are only briefly or occasionally seen. (This may have been true, for example, of the Meta specimen referred to *A. huilae* above.) Preserved specimens compound the dilemma already posed. Pattern or lack of pattern may be due entirely to the preservative, or to its strength. Specimens done in strong formalin tend to a muddy uniformity; many of the older specimens in collections are of this type. It is fortunate that none of the specimens considered in this paper are of so inferior a quality. Nevertheless, they have been preserved by different individuals with different preferences in technique. The preserved specimens are therefore only minimally comparable.

But even the available descriptions of color in life are imperfectly comparable. They were not made to be checked against one another, and they therefore do not stress quite the same details. They were never checked against the same color standards.

Yet it is quite clear that enough information exists to assure us that differences exist. While no possibility exists of entirely avoiding error, some plausible conclusions may be drawn.

Color in anoles is best discussed by breaking it into components. It is a fact about *Anolis* in general that dewlaps are least modified by color change and most readily interpretable in preserved specimens. This fact quite accords with the view (e.g., Rand and Williams, 1970; Williams and Rand, 1977) that the dewlap is an intra- and interspecific signal which should have high constancy in order

always to convey the same message. (A caveat: this rule may have less validity in mainland *Anolis* than it appears to have in the species of the islands.)

In the present case we have the following evidence of dewlap color:

punctatus punctatus (Surinam)

— yellow ochre with white scales (Hoogmoed). The other reports from the range of subspecies (Sergipe, Espírito Santo) stress a yellow color also.

punctatus 'boulengeri'

— orange to reddish-orange (Dixon and Soini). Clearly a deeper shade than in *punctatus punctatus,* but not sharply different. Preserved specimens of both taxa show only light skin and scales.

vaupesianus

— 'black' (Pyburn); 'mulberry red' (Medem) presumably on the authority of the collector: 'greenish' in the female; Medem, in this case himself the collector. There is an obvious discrepancy here, but we are evidently dealing with a dark dewlap, and the dewlap skin in all preserved specimens is darkly pigmented.

From these notes it is clear that *vaupesianus* is sharply distinct in dewlap color from the animals that in size and morphology it most resembles, western *A. punctatus,* and from *A. huilae.* The dewlap of the latter, with dark spots placed in lines or randomly, is quite unlike any of the others. Insufficient information exists for any really useful discussion of dewlap color in the other taxa.

As regards body color, I am very uncertain what can be inferred. From the descriptions of Hoogmoed for Surinam and of Dixon and Soini for Peru, it would appear plausible that a purple phase exists in western *A. punctatus* which does not occur in *A. vaupesianus,* but Vanzolini has not noticed such a purple phase in the *punctatus* of Amazonia and eastern Brazil *punctatus* that he has caught. Absence of purple may therefore not be fully diagnostic for *vaupesianus.* Other aspects of the color of *vaupesianus* involve tints and special aspects of its color repertoire which again are of uncertain value. Size, body, and dewlap color seem safer guides to identification. For *A. huilae* we do not know enough about color repertoire to evaluate the colors in life that we do know. The bold flank spotting seen in *huilae may* be useful, like the nape spot, but neither are obvious in females and are not mentioned in some of the descriptions of colors

in life. See above for discussion of the specimen from Meta. For *nigropunctatus, caquetae, santamartae,* and *deltae,* discussions of preserved body color are of very dubious value. Are the spots of preserved *nigropunctatus* surely of diagnostic value? There is at present no way to tell. The light line in *santamartae* from suboculars to ear seems distinctive. It is less evident in the type than in the other darker specimens. It may or may not be readily visible in life. For these last four species body color cannot be disregarded but determination of specimens must depend upon size, scale characters, and *locality.* Let us look at these features in sequence.

Size

A. vaupesianus, A. huilae, and *A. nigropunctatus* are all within the size range of *A. p. punctatus* (70–80+ mm snout to vent length). *A. dissimilis, A. caquetae, A. santamartae,* and *A. deltae* are, on present evidence, smaller (50–60 mm) (Table 1). (I include in these tables and discussions all described members of the *punctatus* group east of the Pacific slopes of the Andes.)

Table 1. Size of *punctatus* group anoles from east of the Andes and from the inter-Andean valleys.

	Maximum male snout to vent length (in mm.)
punctatus	85
transversalis	83
vaupesianus	82
huilae	82
jacare	73
nigropunctatus	72
deltae	58
caquetae	57
dissimilis	56
santamartae	55

Scale characters

The more significant of these may be examined one by one:
Ventrals: In *Anolis* it is probable that smooth ventrals are

primitive, keeled ventrals the derived condition. (The argument derives from the apparently more frequent correlation of smooth than keeled ventrals with other characters considered primitive; this is not a strong argument.) Most *punctatus* group species have smooth ventrals, but a few have strong keels on the venter. Table 2 again lists the conditions of the several species east of the Andes or in the inter-Andean valleys.

Table 2. Ventral scales in *punctatus* group anoles from east of the Andes and from the inter-Andean valleys.

punctatus	smooth *or* weakly to strongly keeled
vaupesianus	weakly keeled
transversalis	smooth
huilae	smooth
jacare	smooth
nigropunctatus	smooth
deltae	smooth
caquetae	weakly keeled
dissimilis	smooth
santamartae	smooth or weakly keeled

Nostril-rostral relationship: This character is somewhat variable within species, but within a narrow range. The *punctatus* group shows only a fraction of the possible range, and each species shows only a segment of this restricted range. The relevant conditions and the species in which these are seen are listed below:

1) *Circumnasal scale* (=nasal) *directly in contact with rostral: nigropunctatus, jacare.*
2) *Circumnasal scale separated* from rostral by a *small* round *undifferentiated scale: nigropunctatus, dissimilis.*
3) A differentiated *anterior nasal* scale present and in contact with rostral (the anterior nasal is characteristically triangular and overlaps posteriorly part of the *circumnasal*): *deltae, huilae.*
4) *Anterior plus an inferior nasal* in contact with rostral: *punctatus, boulengeri, transversalis, vaupesianus, caquetae, huilae, santamartae.*

It is noteworthy that, while a species may exhibit two of these four categories, these are always adjacent ones and no species is

known to range the full gamut. This character will *assist* in discriminating species.

Snout protuberant or not in males: This character, well known in *A. punctatus,* is clearly present in *A. vaupesianus,* less obvious in *nigropunctatus,* and absent in the other taxa. It again *assists* in identifying species.

Scales across the snout between second canthals: The range in the *punctatus* group is moderate, most species ranging between 6 and 9, *transversalis* including, however, values as low as 4, and *caquetae, nigropunctatus* and *vaupesianus* reaching 10. Very low counts here may point to *transversalis.* Counts otherwise are not diagnostic.

Scales between the semicircles: the minimum number between the semicircles is 0, usually implying broad contact. In the species set as a whole the modal conditions are 0 and 1; a count of 2 is relatively infrequent. This character cannot be relied on to distinguish species.

Loreals: The maximum number of loreals (counted down from the second canthals) may be as low as 3 (*transversalis*) or as high as 7 (*vaupesianus*). More frequently the count ranges from 4 to 6. Again, a very low number of loreals may point to *transversalis,* but in general loreals are not diagnostic.

Interparietal: A very large interparietal in contact with the semicircles is a distinguishing feature of the unique type of *caquetae* and of the type series of *santamartae* and of *dissimilis* and *deltae.* An interparietal smaller than the small ear is characteristic of *nigropunctatus* (clearly so only in the type). For the other members of the *punctatus* group the interparietal is not diagnostic.

Number of supralabials to the center of the eye: The exceptional number of 11 is distinctive for *A. dissimilis.* A range of 6 to 9 is characteristic for all the other species and hence does not discriminate among them.

Lamellae under phalanges ii and iii of fourth toe: Number of toe lamellae in *Anolis* correlates with two factors—perch and size. In the known cases, *punctatus* group anoles tend to high perches—usually in the crown—and should have high lamellar counts for their size. Correspondingly, the better-known, larger species, known to correspond to expectations in perch—*punctatus, vaupesianus*—have counts in the mid- to upper 20s. *A. nigropunctatus, A. jacare,* and *A. huilae* have relatively low counts for *punctatus* group animals of their size (20–24).

Tail crests: Two species—*dissimilis* and *deltae*—have tail crests and hence are unique in the group. Others have a double row without a crest.

Species Diagnoses

What combinations of characters diagnose the *punctatus* group species I have described herein and the others previously described? (See also Tables 3 and 4.)

1) *Vaupesianus* is distinctive in its *black dewlap, strongly protuberant snout* in males, *weakly keeled ventrals,* and *moderate size.* (Distribution: Vaupés and Amazonas.)
2) *Huilae* is distinctive in its spotted or streaked dewlap, and (usually) in the *vivid mottling* of its flanks and in its *moderate size (ventrals smooth).* (Distribution: the upper Magdelena valley in Huila and Tolima, perhaps at high elevations on the eastern slope of the Andes in Meta [Manzanares].)
3) *Santamartae* is distinctive in the large *interparietal broadly in contact with the semicircles,* plus *smooth* or *weakly keeled ventrals, small size,* and *a light line from supralabials to ear and from ear to upper arm.* (Distribution: south slope of Santa Marta mountains.)
4) *Caquetae* is diagnosed by its *large interparietal broadly in contact with the semicircles,* plus *keeled ventrals, small size,* and no light line from suboculars to ear. (Distribution: known only from the Upper Apaporis in Caquetá, Colombia.)
5) *Nigropunctatus* stands out by its *small interparietal, smaller than the small ear,* an irregularly and weakly punctate pattern on the flanks (in males on middorsum also), *snout protuberant in males,* and by *moderate size (ventrals smooth).* (Distribution: from Norte de Santander in Colombia to Táchira and Trujillo in Venezuela.)
6) *Deltae* has the *large interparietal broadly in contact with the semicircles* and *small size* of *caquetae* but has *smooth ventrals,* a *tail crest* and a *short, blunt head.* (Distribution: Delta of the Orinoco in Venezuela.)
7) *Dissimilis* has a very *large interparietal in contact with the semicircles, small size, smooth ventrals* and *tail crest* like those of *deltae,* but a *strikingly elongate head.* (Distribution: Madre de Dios in Peru.)

8) *Jacare* is distinctive in *moderate size,* male *without a protuberant snout,* with an *immaculate yellow dewlap* and a strongly *reticulate body pattern* with often an oblique light streak from the throat to above the shoulder; *female* with *unspotted body* and *unmarked throat* (ventrals smooth). (Distribution: the Sierra Madre de Mérida in Venezuela.)
9) *Transversalis* is like *jacare* in *moderate size* and the *lack of a protuberant snout in males,* but the male has a *yellow dewlap with streaks and spots,* and a *body pattern of oblique light lines enclosing rows of black spots;* and females with *bold transverse bands on the body* and the *throat vividly cross-marked with black* (*ventrals* smooth). (Distribution: western Amazonia.)
10) *Punctatus* has *moderate size* and a *strongly protuberant snout* in males and a yellow or orange dewlap. (*Ventrals smooth* or *keeled*). (Distribution: Amazonia, the Guianas, and the Atlantic Forest of Brazil.)

The Geography of Difference

The species of the *punctatus* group that have been discussed here are all those thus far reported that are east of the Andes or inter-Andean. (For convenience, *santamartae* is counted in this group; it lies in an eastward-looking valley in the southern part of the isolated Sierra Nevada de Santa Marta.) This assemblage, as it turns out, is, if not a natural group, clearly as natural as a group which also includes taxa west of the Andes, currently referred to the *punctatus* species group. None of the western species are demonstrably close to the species here considered.[1]

[1]I no longer consider *A. nigropunctatus* to be especially close to A. *nigrolineatus* (Williams, 1965). *A. nigropunctatus,* as will be suggested below, is probably closer to *A. jacare,* and *A. nigrolineatus* may be a strict synonym of *A. festae* Peracca (syntypes examined). Both nominal species have the same highly peculiar dewlap with an elongate dark spot. There are no scale differences. There is variability in head shape. The sole known differences between southern Ecuadorian specimens (Machala, El Oro) known from recent large collections by Fitch, Echelle and Echelle, and northern populations (Pichincha) known from equally large collections made by Kenneth Miyata are smaller size in the northern populations (Miyata, personal communication) and a blue iris in the north (Miyata) as compared with the yellow iris reported by Fitch *et al.* (1976) for southern animals. No recently collected animals—live or preserved—show the narrow dark middorsal line believed diagnostic for *A. nigrolineatus.*

Table 3. Scale variation in *punctatus* group anoles—inter-Andean or east of Andes.

	transversalis	*punctatus*	*vaupesianus*	*huilae*	*jacare*
sample size	N = 38	N = 157	N = 6	N = 17	N = 24
dewlap in ♀	+	–	–	–	–
snout swollen in ♂	–	+	+	–	–
scales across snout	4–8	7–14	8–10	8–11	6–8
nasal/rostral	anterior and inferior nasal in contact with rostral	anterior and inferior nasal in contact with rostral	anterior and inferior nasal in contact with rostral	anterior and inferior nasal in contact with rostral	circumnasal in contact with rostral
scales between semicircles	0–1	0–3	0–2	0	0–2
loreal rows	3–6	4–8	5–7	4–5	4–7
interparietal/ear	>>	>/<	>/>>	>/<	>
scales between interparietal and semicircles	0–3	(0)–(5)	2–3	0–3	1–3
scales between suboculars and supralabials	0	0	0	0	0
supralabials to center of eye	6–9	6–10	7–9	5–7	7–9
lamellae under fourth toe	22–27	22–30	22–25	20–24	19–25
ventrals	smooth	keeled *or* smooth	weakly keeled	smooth	smooth
tail crest	–	–	–	–	–
size	83	85	80	82	73

Table 3 *(continued)*

	nigropunctatus	*santamartae*	*caquetae*	*deltae*	*dissimilis*
sample size	N = 4	N = 3	N = 1	N = 1	N = 1
dewlap in ♀	–	–	?	?	?
snout swollen in ♂	(+)	+	+	–	–
scales across snout	7–10	4–6	10	8	7
nasal/rostral	circumnasal in contact with rostral *or* separated by *1* scale	anterior and inferior nasals in contact with rostral	anterior and inferior nasals in contact with rostral	anterior nasal in contact with rostral	circumnasal separated from rostral by 1 rounded scale
scales between semicircles	0–2	0	1	0	0
loreal rows	4–6	4–5	5	4	4
interparietal/ear	<	>>	>>	>>	>
scales between interparietal and semicircles	1–4	0	0	0	0
scales between suboculars and supralabials	0	0	0	0	0
supralabials to center of eye	7	7	7	7	11
lamellae under fourth toe	21–22	18–21	22	24	17
ventrals	smooth	smooth or obtusely keeled	weakly keeled	smooth	
tail crest	–	–	–	+	+
size	72	55	57	58	56

Table 4. Scale variation in *Anolis punctatus*.

	Colombia N = 4	Ecuador N = 38	Peru N = 46	Bolivia N = 6	Guyana N = 8	Surinam N = 7	Brasil N = 48
scales across snout	8–11	7–12	7–14	9–13	9–11	8–11	7–14
scales between supraorbital semicircles	0–2	0–2	0–2	1–3	1–2	0–2	1–2
loreal rows	5–8	4–7	5–7	5–8	4–6	5–6	5–7
interparietal/ear	>	>	>/<	≥	>/<	≥	>/<
scales between interparietal and semicircles	2–4	1–4	(0)–(5)	2–4	2–4	1–3	1–3
supralabials to center of eye	6–8	6–9	6–9	8–10	7–10	7–10	6–9
lamellae under fourth toe	24–25	24–29	22–29	25–29	23–26	24–25	22–30
ventrals	keeled	keeled	keeled or smooth	smooth	keeled or smooth	smooth	keeled or smooth

The eastern and inter-Andean assemblage is, itself, clearly morphologically heterogeneous, showing several levels of differentiation. Yet it is a striking fact that only one of the 11 forms here called species is widely sympatric with any of the others: *A. transversalis* occurs within the range of *A. punctatus* and *A. vaupesianus.* It is abundantly distinct not only from the two taxa with which it is sympatric, but from *all* other *punctatus* group species. It differs not only in the striking color characters emphasized in the section immediately above, but it stands at one extreme in scale characters also (low counts of loreals and scales across the snout).

None of the other nine described forms is known to co-occur. Two of them, however, are in their own way sharply distinct. *A. dissimilis,* as its name implies, seemed very distinct when it was first made known, but the tail crest, otherwise unique within the *punctatus* group, has since been found in widely allopatric *deltae* (which differs, however, *inter alia,* in its much shorter head).

The remaining taxa are allopatric; they do, however, divide into low-land and high-land forms, and this, while it is not prima facie evidence against conspecificity, makes it a little less likely.

The low-land species are *punctatus, vaupesianus,* and *caquetae.* Here it is clear that as regards the first two I have relied on color in life. The difference, however, is sharp, and, if there are any intermediate populations, we can specify where they must be: in Amazonas between the Ríos Putumayo and Caquetá.

It is, of course, crucial to the final allocation of all allopatric taxa that are phenetically similar that, when possible, we endeavor to discover whether there is a contact zone and to determine what happens there. I have expressly chosen not to call distinctive populations subspecies merely because they are related. Unless variation is clinal and the relevant characters not congruent—in which case taxonomic description is not warranted—the alternative to the hypothesis of allospecies, which I am using here, is subspecies, a highly restrictive hypothesis according to which distinctive populations with congruent characters meet in well-defined zones of intergradation. I agree with the long-expressed opinion of Wilson and Brown (1953) that these restrictive conditions are rarely met. *A. punctatus* and *A. vaupesianus* are, indeed, distinctive populations but closest relatives that are either allospecies, the ends of a cline, or supspecies. There is not present evidence of clinal change or of

intergradation. My decision therefore is to tentatively regard the two populations as allospecies.

The case of *A. caquetae* is different. It is a single specimen peculiar in some aspects of color and squamation—in combination *outside* the known limits of other forms. As a single specimen, it is not clearly representative of any distinctive population. None of its characters is individually unusual within the broad variation of the *punctatus* group. The *large* interparietal in contact with supraorbital semicircles is not at all usual in the *punctatus* species group, but see *A. santamartae.* The color *as preserved* is distinctive but suffers the difficulty of preserved color in *Anolis,* discussed at some length above. Clearly, acceptance of *A. caquetae* as a valid species involves risk of error. But if it were to be synonymized, what would it be synonymized with? *A. punctatus* or *A. vaupesianus*? Or would both sink into a variable species to be called *A. punctatus*? The large interparietal in contact with semicircles is rare in *A. punctatus* (one known case in 157 specimens), unknown in *A. vaupesianus* (but the sample is too small for a secure statement). It is closer to *A. vaupesianus,* but it would seem erroneous on present evidence to synonymize *A. vaupesianus* with *caquetae.* The case here is one of inadequate evidence, and, above all, of inadequate search for evidence. The fauna of Ríos Vaupés, Caquetá, and Putumayo and their tributaries is very poorly known.

The remaining taxa with which we are concerned—*jacare, nigropunctatus, huilae,* and *santamartae*—are all animals of high elevations. Of these, only *jacare* is an old name, and *huilae* and *santamartae* have been described herein.

Santamartae is the most distinctive of these. In the tendency to keeling of the ventrals and the light line from the labials toward the ear it is unlike the others. It seems also to be smaller.

The other three, it must be confessed, are primarily distinctive in coloration. *A. huilae* seems to stand out in this series. The bold light spotting and nape spot in males, as well as the contact of differentiated anterior and inferior nasals with the rostral, contrast with the dark spotting of *nigropunctatus* and the vermiculation of *jacare* and with the primitive circumnasal scale characteristic of both the latter.

Between *jacare* and *nigropunctatus* there are no conspicuous scale differences other than the smaller interparietal of *nigropunctatus* (but this is sharply evident only for the male type of *nigropunctatus,*

the only known male). They differ, however, in color; the sparse dark spots of *nigropunctatus* are quite unlike the bold vermiculation of male *jacare*. I am reinforced in my confidence of this color character by examination of a series of 11 specimens of *jacare* from three localities in the state of Merida made available to me by James R. Dixon. The males seem clearly distinctive; the females are not as readily assigned. Between these two, however, and even between *nigropunctatus* and *huilae,* there might be a contact zone. The appropriate intermediate regions remain uncollected.

I have not here gone beyond a minimal analysis of the phenetic similarities of the 10 species of the eastern *punctatus* species group. I do not attempt any history or even any dendrogram of relationship. It seems to me totally premature to do so.

Of the 10 species only three—*punctatus, transversalis,* and *jacare*—have been known for more than 15 years. Of these, only *punctatus* is widespread and relatively common. *A. transversalis* is widespread but rather scarce in collections, although the collections of Pekka Soini (Soini and Dixon) indicate that it must be moderately common, at least in the Iquitos region. *A. jacare* is known only from the Merida region in Venezuela where, from the experience of Carlos Rivero Blanco and Williams (Williams *et al.,* 1970, and the recent collections by James Dixon), it is commoner than the infrequent sightings of it and the meager collections indicate.

Anoles of the *punctatus* group are animals usually of the canopy and appear rather infrequently on the trunks or near the ground (*A. huilae fide* Dennis Harris may be an exception since it is, according to his report, more of a trunk-ground adapted species like *A. frenatus* [cf. Scott *et al.,* 1976 for the latter]). Most of them are, therefore, not conspicuous lizards, whatever their real abundance.

Other species may be genuinely rare, rare enough that the question of intraspecies and interspecies, even intergeneric competition, becomes moot. It is difficult, however, to demonstrate that failure to observe is equivalent to real rarity. Many species of *Anolis* also are highly cryptic and behaviorally highly adapted to crypsis, almost never visible unless they move. Some, readily capturable while sleeping and therefore known to be at least locally common, are rarely seen in the daytime, and their diurnal activity and ecology are therefore almost unknown.

However, quite apart from any characteristics of the animals that may make acquisition of knowledge about them difficult, a primary and evident difficulty is failure to explore and to collect. *Anolis huilae* is not only a species just now described, but only very recently collected. Dennis Harris is the collector of all the Tolima specimens —23 obtained in one 10-day trip which did not specialize in *Anolis* but sought lizards of all kinds. Such a collection in a brief span implies that prior sampling of this area, which has not been totally neglected—it is the type locality of *Anolis tolimensis* and *A. ibague* - has nevertheless been quite inadequate.

If this is true of areas from which there is moderately good representation in old collections, what may still be coming from areas that are still altogether or nearly untouched?

The Department of Nariño is one such area. Collections by even Ayala's group have been only in the low-lands near Tumaco; there is no reason to believe that even near Tumaco there is not much more to find.

An undescribed species is known from the west side of the Sierra Nevada de Santa Marta, and one on the south side has been described herein. What occurs on the east side? Are the new species the only ones on the west and south sides? Is the fauna of the Chocó completely known, of Cauca, Antioquia, Bolívar, Santander, and Norte de Santander? One can, in fact, call the roster of the Departments of Colombia and it will not be possible to say even of the relatively well collected areas that the herpetofauna is completely known. We in fact do not know enough to estimate the fraction that is unknown. (However, to shirk the frustrating effort of dealing with incomplete and inadequate evidence would be to acquiesce in the perpetuation of ignorance. Our obligation is, while not avoiding these thorny thickets, to explore carefully and to leave the paths that we pursue plainly marked.)

What has been done in this paper is to attempt—and I do not vouch for more than an attempt—to answer the first and most elementary (but most fundamental) of biological questions: *who?* - i.e., what is the cast of characters? After we have answered this first question we may begin to ask the question *where?* On the way we may begin to answer other questions: *what does it do? with whom does it interact?* Much later, when the picture is much clearer, we can try to answer historical questions: how did this *system* come about. On the evidence before us the picture is too incomplete, the

unfilled places in the evidence too blatant and glaring, to begin an analysis of species group history or even, in any serious sense, of inter-group relationship. We do not yet know enough to ask the right questions.

ACKNOWLEDGMENTS

I am indebted to William F. Pyburn for permission to describe the new species collected by him, and to Alan E. Leviton (California Academy of Sciences [CAS]), Pedro Ruiz (Instituto de Ciencias Naturales, Bogota [ICN]), William E. Duellman (University of Kansas Museum of Natural History [KU]), James Dixon (Texas A & M University), and Jean Lescure (Museum National de Histoire Naturelle, Paris [MNHP]) for permission to examine material in their charge. Crucial to the study was newly collected material made available by Stephen Ayala, Dennis Harris, and William Lamar. Stephen Ayala also prepared the distribution map. Laszlo Meszoly in preparing the figures has done me an indispensible service.

LITERATURE CITED

Dixon, J. R., and P. Soini. 1975. The reptiles of the Upper Amazon Basin, Iquitos Region, Peru. I. Lizards and amphisbaenians. Contrib. Biol. Geol. Milwaukee Public Mus. No. 4, pp. 1–58.

Fitch, H. S., A. F. Echelle, and A. A. Echelle. 1976. Field observations on rare or little known mainland anoles. Univ. Kansas Mus. Nat. Hist. Sci. Bull., **51**: 91–128.

Greene, H. W. 1977. Lizards of the genus *Uracentron* (Iguanidae) in east-central Colombia. Herpetologica, **33**: 256–260.

Hoogmoed, M. S. 1973. Notes on the herpetofauna of Surinam. IV. The lizards and amphisbaenians of Surinam. The Hague, W. Junk, 410 pp.

Rand, A. S., and E. E. Williams. 1970. An estimation of redundancy and information content of anole dewlaps. Amer. Nat., **104**: 99–103.

Scott, N. J. Jr., D. E. Wilson, C. Jones, and R. M. Andrews. 1976. The choice of perch dimensions by lizards of the genus *Anolis* (Reptilia, Lacertilia, Iguanidae). J. Herp., **10**: 75–84.

Williams, E. E. 1965. South American *Anolis* (Sauria, Iguanidae): Two new species of the *punctatus* group. Breviora Mus. Comp. Zool. No. 233, pp. 1–15.

———. 1974. South American *Anolis:* Three new species related to *Anolis nigrolineatus* and *A. dissimilis*. Breviora Mus. Comp. Zool. No. 422, pp. 1–15.

Williams, E. E., and A. S. Rand. 1977. Species recognition, dewlap function, and faunal size. Amer. Zool., **17**: 261–270.

Williams, E. E., O. A. Reig, P. Kiblisky and C. Rivero-Blanco. 1970. *Anolis jacare* Boulenger, a solitary anole from the Andes of Venezuela. Breviora Mus. Comp. Zool. No. 353, pp. 1–15.

Williams, E. E., and P. E. Vanzolini. 1980. Notes and biogeographic comments on anoles from Brasil. Pap. Avuls. Zool. S. Paulo, **34**: 99–108.

Wilson, E. O., and W. L. Brown, Jr. 1953. The subspecies concept and its taxonomic application. Syst. Zool., **2**: 97–111.

LIBRARY
MAR 1 8 1985
HARVARD
UNIVERSITY

BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 30 JUNE 1982 NUMBER 468

A NEW FOREST SKINK FROM PONAPE

A. ROSS KIESTER[1]

ABSTRACT. *Emoia ponapea,* new species, is described from Ponape in the Caroline Islands where it inhabits deep forest. It is distinguished from all other *Emoia* by the presence of 13 premaxillary teeth and a palate intermediate between the alpha and beta conditions.

INTRODUCTION

A survey of the scincid genus *Emoia,* undertaken after a collecting trip to Ponape in the Caroline Islands and other localities in Micronesia, showed that three specimens taken on Ponape represent a distinct species of *Emoia.* In fact, as discussed below, this form possesses some characters which make its generic allocation somewhat problematic. However, an analysis of the boundaries of the genus *Emoia* is beyond the scope of this paper, and so the new taxon is here described as:

Emoia ponapea, new species
(Figs. 1–5)

Holotype: MCZ 121041, forest 1/4 mile above Agricultural Station, Kolonia, Ponape Island, Eastern Caroline Islands. Collected by A. R. Kiester, 28 July 68.

Paratypes: Eastern Caroline Islands, Ponape Island: MCZ 121042-43, same data as for holotype (The skull of 121042 has been removed and prepared. This individual was a sexually mature

[1]Smithsonian Tropical Research Institute, APO Miami 34002.

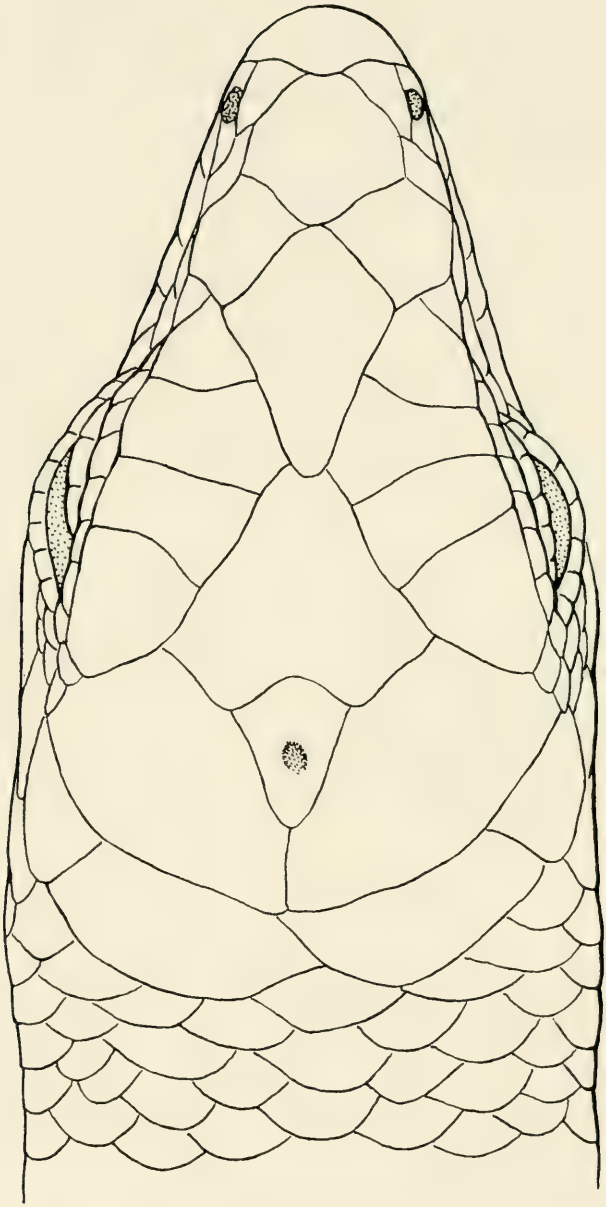


Figure 1. Head scalation of the holotype (MCZ 121041) of *Emoia ponapea*. Dorsal view.

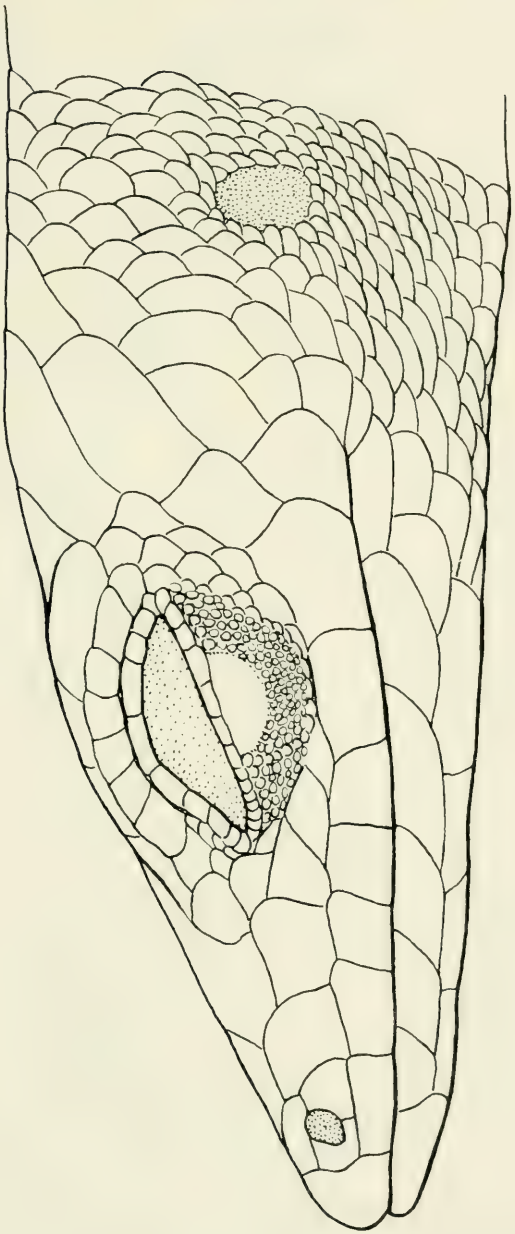


Figure 2. Head scalation of the holotype (MCZ 121041) of *Emoia ponapea*. Lateral view.

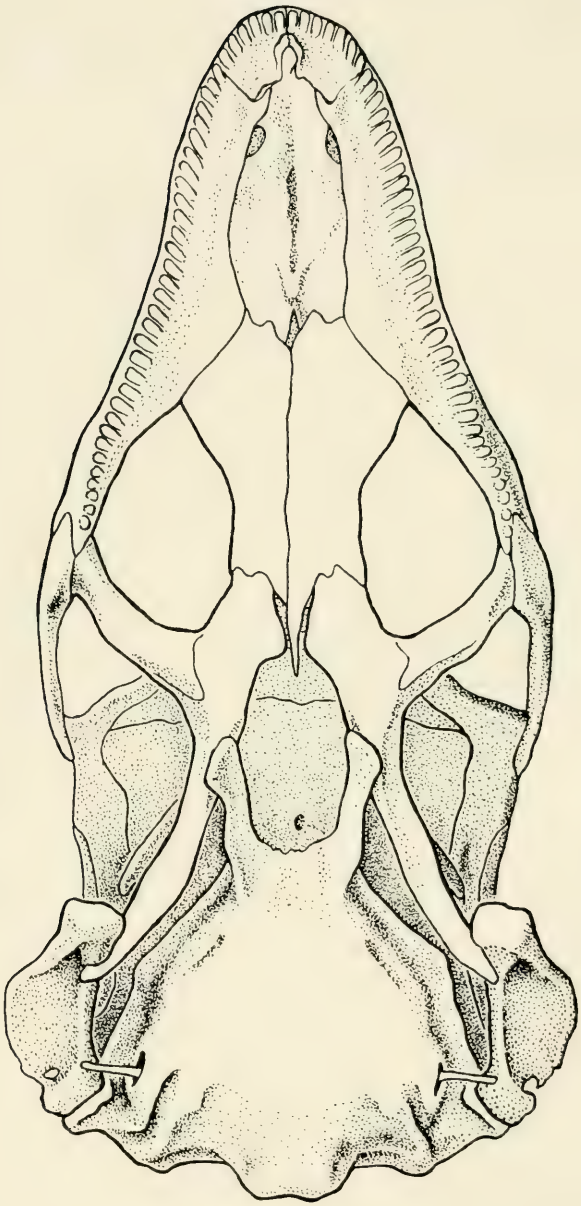


Figure 3. Skull of paratype (MCZ 121042) of *Emoia ponapea*. Ventral view.

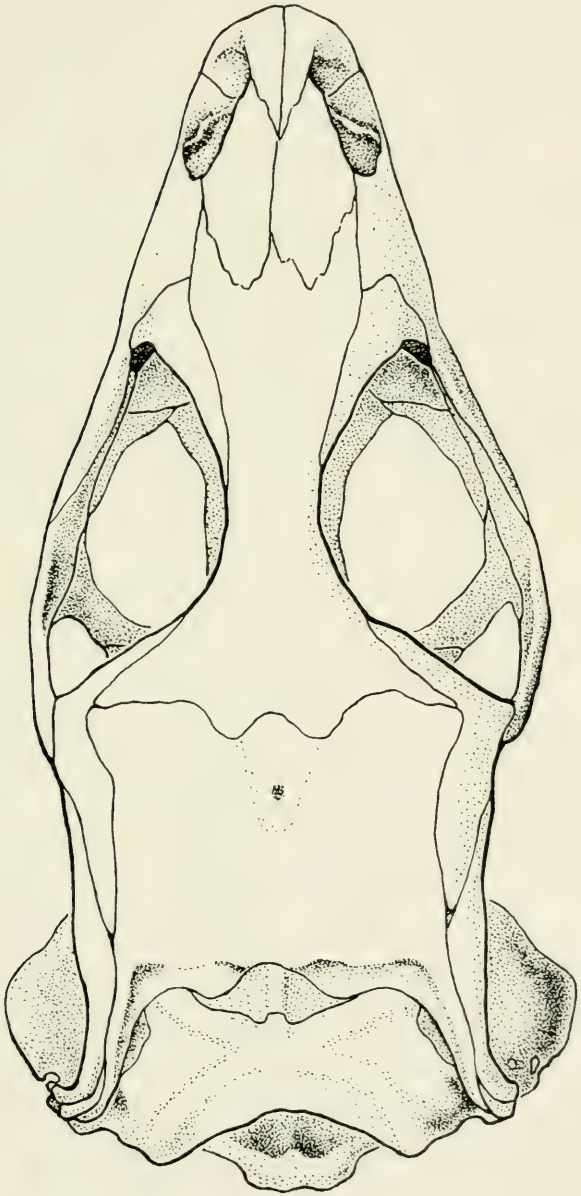


Figure 4. Skull of paratype (MCZ 121042) of *Emoia ponapea*. Dorsal view.

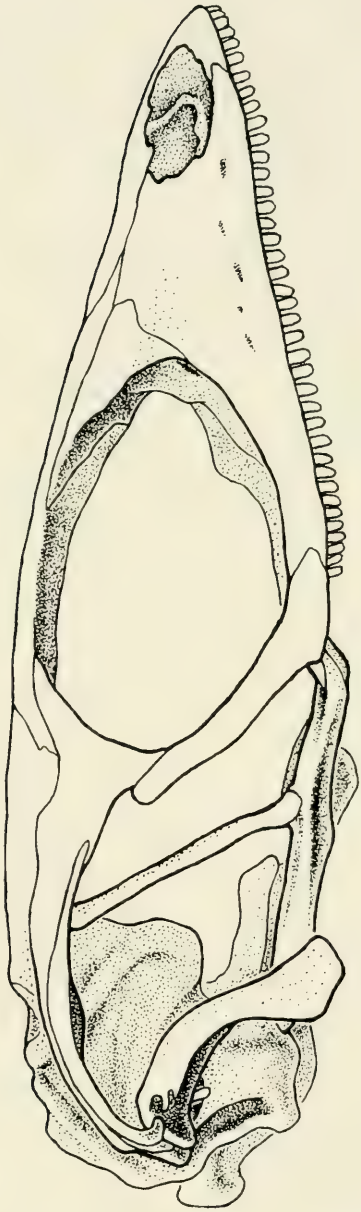


Figure 5. Skull of paratype (MCZ 121042) of *Emoia ponapea*. Lateral view.

female.); USNM 138985-86, Nanpil River; USNM 138991, Dolonier; USNM 139002-05, N end of ridge parallel to Tavensorola River; USNM 139006-07, Dolen Eirike; CAS 152222 (formerly USNM 138987), Nanpil River. All USNM and CAS specimens collected between 13 September 55 and 5 December 55 by J. T. Marshall, Jr. See acknowledgments for abbreviations.

Diagnosis: A member of the genus *Emoia,* as it is currently and broadly construed (Greer, 1974), differing from all other members of the genus by the possession of 13 premaxillary teeth. It is distinguishable externally by the combination of the following characters: interparietal present; subdigital lamellae of the 4th toe 38–46; midbody scale rows 30–32; middorsal scale rows 48–54 counting from the nuchals to the anterior insertion of the hind limb and 52–60 counting to the point directly above the vent; body form small (snout-vent length less than 50 mm) and distinctly slender; head narrow and relatively pointed; coloration without metallic blues or greens.

DESCRIPTION OF HOLOTYPE

The range of paratypical variation is given in parentheses after the description of the holotype character.

General Appearance: Body small with a snout-vent length of 46 mm (21 mm to 49 mm for the paratypes), form distinctly slender and gracile. Tail long, over 1.5 times the snout-vent length. Limbs well developed, overlapping easily when adpressed to the body; hindlimb length 23 mm, forelimb length 13 mm. Five digits on each foot.

Head and Head Scalation (Figs. 1–2): Head narrow and somewhat depressed. Rostral twice as long as deep; supranasals separated, much wider anteriorly than posteriorly; prefrontals moderately to narrowly separated by frontonasal and frontal; supraoculars 4; frontoparietals fused; interparietal single, distinct, and large; one pair of parietals in contact behind interparietals; two pairs of temporals corresponding to the primary and secondary temporals of Taylor (1935) with only the secondary temporals placed toward the top of the head; supraciliaries 9–9; loreals two; single pair of nuchals; 6th supralabial subocular; nasal divided below nostril; eyelid window undivided; postmental contacts first two infralabials on each side.

Ear: Tympanum sunk below level of epidermis. A single larger anterior lobule with two smaller ones below (a single smaller one on one side of one of the paratypes). Vertical (longest) diameter of ear opening 1.1 mm.

Body Scalation: Scales smooth. Midbody scale rows 30 (30–32). Middorsal scale rows 48 (48–54) counting from the first scale posterior to the nuchals to the anterior insertion of the hind leg and 53 (52–60) counting posterior to a point directly above the vent. Subdigital lamellae on the 4th toe of the hind foot rounded with 42 on both sides (38–46). Preanals not enlarged.

Coloration: Dorsum with a central tan stripe with irregular edges extending from the snout to the end of the tail. A small number of black spots on the stripe on the head (some of the paratypes show black spotting on the stripe on the back as well). A poorly defined laterodorsal stripe on either side of this beginning behind the eye and extending one third of the way down the tail. These stripes are formed by two irregular rows of black dashes on the tan color. Sides reddish brown becoming spotted over cream color toward the venter. Limbs reticulated brownish red over cream above. Chin, throat, venter, and undersides of limbs and tail all immaculate cream.

DESCRIPTION OF SKULL

Skull MCZ 121042, paratype (Figs. 3–5): General appearance very delicate and somewhat narrow (as compared, say, to a similarly sized *E. cyanura*). Premaxillary teeth 13. Secondary palate moderately well developed. Palatines meet extensively along the midline and send pointed projections posteriorly between the anterior portions of the pterygoids. One of the projections is folded slightly under the other. Pterygoids intermediate in condition between the alpha and beta configurations of Greer and Parker (1968) and Greer (1974), with the anterior portion showing distinct expansion toward the midline without achieving a strongly recurved process.

Lower Jaw: The Meckelian canal is as the second of the two conditions described by Greer (1974) for the *Leiolopisma* group of lygosomine genera: canal closed with no suture evident.

DISTRIBUTION AND ECOLOGICAL OBSERVATIONS

At present this species is known only from the island of Ponape in the Caroline Islands. Ponape is also known as Ascension Island in some of the older literature.

All three MCZ specimens were collected in the late morning on the floor of a mature forest in an area where sun flecks occurred. No other emoias were seen in this deep forest habitat. *E. cyanura, E. caeruleocauda,* and *E. boettgeri* were found only in more open areas towards the coast. Ecological notes by J. T. Marshall, Jr. accompanying the other specimens indicate that they were also collected on the floor of the forest. This species bears a similar ecological relationship to its congeners as *E. parkeri* does to the other emoias in the Fiji Islands (Brown *et al.*, 1980).

Two of the USNM specimens are hatchlings. Marshall notes that the eggs were collected on 27 October 55 in a rotted palm stump in the rain forest and that they hatched on 6 November 55. A clutch size of two is typical for most species in this genus (Greer, 1968).

DISCUSSION

The current state of confusion in the genus *Emoia* prevents any accurate assessment of the relationships of *Emoia ponapea.* A thorough revision of the genus would be necessary to understand the relationships of any but the most closely related of its species. Lacking this, a comparison with the smaller emoias found in Micronesia may be useful. *E. cyanura* and *E. caeruleocauda,* both also found on Ponape, have true beta palates. This character is considered derived in the genus (Greer, 1974), as is the very high subdigital lamellae count of *cyanura* itself. Thus, since *E. ponapea* has a palate intermediate between the alpha and beta conditions, it is unlikely that it is derived from any of the members of the *cyanura* group directly. Within Micronesia a possible candidate for a related species could be *E. mivarti.* However, there are notable differences from this species as well. *E mivarti* has the interparietal fused with the frontoparietal and is a much stouter animal. None of these species seems closely related to *E. ponapea;* a search for its relatives will have to extend outside of Micronesia.

The most unusual character of *E. ponapea* is the possession of 13 premaxillary teeth. All other members of the genus *Emoia* have 11, as do all of the genera regarded as related to *Emoia* (the members of Group II of Greer, 1974). The only other leiolopismid genus with 13 premaxillaries is *Carlia,* which is clearly unrelated on other grounds (Greer, 1974). For the genus *Emoia* this character state must be derived. This character and the intermediate condition of the palate argue that *E. ponapea* is rather different from the rest of the genus. Just how different it really is will have to be determined by future work.

ACKNOWLEDGMENTS

I wish to thank W. C. Brown, Allen Greer, the late T. Preston Webster, and Ernest E. Williams for much help and discussion on matters related to this paper. The illustrations are by Lazlo Meszoly. This work was supported by the Evolutionary Biology Committee of Harvard University, The Society of Sigma Xi, and Ernest E. Williams. For permission to examine specimens in their care, I thank A. G. C. Grandison, British Museum (Natural History); H. Marx, Field Museum of Natural History; A. Leviton, California Academy of Sciences (CAS); Ernest E. Williams, Museum of Comparative Zoology, Harvard University (MCZ); R. Stebbins, Museum of Vertebrate Zoology, University of California at Berkeley; and the late J. Peters and W. R. Heyer, United States National Museum (USNM).

LITERATURE CITED

Brown, W. C., J. C. Pernetta, and D. Watling. 1980. A new lizard of the genus *Emoia* (Scincidae) from the Fiji Islands. Proc. Biol. Soc. Wash., **93**: 350–356.

Greer, A. E. 1968. Clutch size in the genus *Emoia.* Copeia, **1968**: 417–418.

———. 1974. The generic relationships of the scincid lizard genus *Leiolopisma* and its relatives. Austr. Jour. Zool. Suppl. Ser. No. 31, pp. 1–67.

Greer, A. E., and F. Parker. 1968. *Geomyersia glabra,* a new genus and species of scincid lizard from Bougainville, Solomon Islands, with comments on the relationships of some lygosomine genera. Breviora Mus. Comp. Zool. No. 302, pp. 1–17.

Taylor, E. H. 1935. A taxonomic study of the cosmopolitan scincoid lizards of the genus *Eumeces,* with an account of the distribution and relationships of its species. Kans. Univ. Sci. Bull., **23**: 1–643.

Webster, T. P. 1969. Aspects of the morphological and ecological variation in the *cyanura* group of the lizard genus *Emoia* (Sauria: Scincidae) in the Solomon Islands. Honors Thesis, Harvard University.

MUS. COMP. ZOOL
LIBRARY
MAR 18 1985
HARVARD
UNIVERSITY

BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 30 JUNE 1982 NUMBER 469

CATALOG OF THE PRIMARY TYPES OF BOMBYLIIDAE (DIPTERA) IN THE ENTOMOLOGICAL COLLECTIONS OF THE MUSEUM OF COMPARATIVE ZOOLOGY, WITH DESIGNATIONS OF LECTOTYPES

NEAL L. EVENHUIS[1]

ABSTRACT. One hundred and nine holotypes, lectotypes, and syntypes of Bombyliidae deposited in the entomological collections of the Museum of Comparative Zoology are listed. Lectotypes are designated for 27 taxa based on material in MCZ.

INTRODUCTION

This catalog lists the primary types of 109 taxa of Bombyliidae located in the entomological collections of the Museum of Comparative Zoology, Harvard University, Cambridge (MCZ). Fifty-seven of these taxa are represented by holotypes, 17 by syntype series, and 35 by lectotypes. All but one of the types listed here are deposited in the general collection of the MCZ. The unique male holotype of *Epibates harrisi* Osten Sacken is deposited in the Thaddeus W. Harris collection, which is maintained separately from the general collection. Twenty-seven new lectotype designations are recorded herein including two by Jack C. Hall, University of California, Riverside. Of the remaining 25 new lectotypes, three are designated in Hall and Evenhuis (1981). The format used here follows that of Radovsky *et al.* (1976) with modifications. Information presented in brackets [ ] is data additional to or corrected from data recorded in the original description. The present combination of each taxon

[1]Department of Entomology, Bishop Museum, P.O. Box 19000-A, Honolulu, Hawaii 96819.

listed, if it differs from the original combination, is also included after the remarks section under each taxon concerned.

The majority of species recorded here were described by Loew in his "Centuries," Osten Sacken in his "Western Diptera," and C.W. Johnson in various publications. Most of the types or type series in the collections carry a red label with a type register number placed there by Nathan Banks when he curated the collection. Recent additions to the type collection carry a similar label with a type number placed there by various curatorial technicians since Banks. Banks' type labeling has posed problems because he sometimes failed to label *all* of the syntypes in a syntype series or labeled *more* than the original description of that particular taxon was based upon (this is especially true for many of Loew's species). In compiling this catalog, all original descriptions were checked to make sure the correct number of syntypes were located and labeled. Discrepancies in the number of specimens found versus the number of specimens upon which that species was based are noted in the remarks section under each taxon concerned. In some cases, syntypes of certain taxa were found to be located in other museums. These museums include the United States National Museum of Natural History, Washington, D.C. (USNM), the American Museum of Natural History, New York (AMNH), the Snow Collection at the University of Kansas, Lawrence (SNOW) and the Zoologisches Museum of the Museum für Naturkunde der Humboldt-Universität, Berlin (ZMHU). This information is supplied in the remarks section under each taxon concerned.

Some syntypes of the bombyliid taxa described by Osten Sacken in "Biologia Centrali-Americana" are deposited in the MCZ. Lectotypes for most of these species were designated by Painter and Painter (1962) from material in the British Museum (Natural History), where in most cases the majority of the syntypes of these particular taxa are housed. Specimens of these species represented in the MCZ carry labels signifying that the lectotype for that species is in the BMNH.

SPECIES-GROUP INVENTORY

adusta Loew, **Anthrax** SYNTYPES 2 ♀ 12672
1869 *Berliner Entomol. Z.* **13:** 26 pin
CUBA: [no further data] Gundlach

The specimens in the MCZ are left here as syntypes pending revision of the genus.
Present name: *Villa adusta* (Loew)

agassizi Loew, **Exoprosopa** HOLOTYPE ♀ 12635
1869 *Berliner Entomol. Z.* **13:** 16 pin
UNITED STATES: California: [no further data] Agassiz

albicapillus Loew, **Bombylius** LECTOTYPE ♀ 12686
1872 *Berliner Entomol. Z.* **16:** 78-79 pin
UNITED STATES: [California]: San Francisco [no date] H. Edwards
Lectotype designated by Evenhuis *in* Hall and Evenhuis (1980: 6).

albidipennis Loew, **Geron** HOLOTYPE ♂ 12713
1869 *Berliner Entomol. Z.* **13:** 174 pin
UNITED STATES: California: [no further data] Agassiz

aldrichi Johnson, **Phthiria** SYNTYPES 2 ♂, 1 ♀ 7555
1903 *Psyche* **10:** 184 pin
UNITED STATES: Idaho: Caldwell 24.IV.1901 C.W. Johnson Collection
These specimens are left as syntypes pending revision of the genus.
Present name: *Phthiria (Poecilognathus) aldrichi* Johnson

alpha Osten Sacken, **Anthrax** LECTOTYPE ♀ 12660
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 239-40 pin
UNITED STATES: Wyoming: Cheyenne 21.VIII. O. Sacken
Four (three male, one female) of the five specimens on which Osten Sacken based his description of *alpha* have been located at the MCZ. The fifth syntype is deposited in AMNH. The best preserved of the MCZ material, the female, is here designated *lectotype.*
Present name: *Poecilanthrax alpha* (Osten Sacken)

amabilis Osten Sacken, **Ploas** LECTOTYPE ♂ 12703
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 261-62 pin
UNITED STATES: California: Yosemite 5.VI. O. Sacken
Osten Sacken based his description of *amabilis* on two female and one male. The male is here designated *lectotype.*
Present name: *Conophorus amabilis* (Osten Sacken)

arenicola Johnson, **Anthrax lateralis** LECTOTYPE ♂ 7548
1908 *Psyche* **15:** 15 pin
UNITED STATES: New Jersey: Clementon 16.V. 1917 C.W. Johnson Collection
Lectotype male and *allolectotype* female designated herein by J.C. Hall.
Present name: *Villa lateralis arenicola* (Johnson)

arizonicus Banks, **Systropus** SYNTYPES 2 ♂ 13484
1909 *Entomol. News* **20:** 18 pin
UNITED STATES: Arizona: Palmerlee [no date] N. Banks Collection
These specimens are left as syntypes pending revision of the genus.

atratula Loew, **Ploas** HOLOTYPE ♀ 12698
1872 *Berliner Entomol. Z.* **16:** 79-80 pin
UNITED STATES: California: [no further data] H. Edwards
Present name: *Conophorus atratulus* (Loew)

atriceps Loew, **Bombylius** LECTOTYPE ♂ 12688
1863 *Berliner Entomol. Z.* **7:** 301 pin
UNITED STATES: Florida: [no further data] O. Sacken
Lectotype designated by Evenhuis *in* Hall and Evenhuis (1980: 15).

aurifer Osten Sacken, **Bombylius** LECTOTYPE ♀ 12691
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 249-50 pin
UNITED STATES: California: Webber Lake 26.VII. O. Sacken
Lectotype designated by Evenhuis *in* Hall and Evenhuis (1980: 18).

banksi Johnson, **Dipalta** HOLOTYPE ♂ 13485
1921 *Occas. Pap. Boston Soc. Nat. Hist.* **5:** 12-13 pin
UNITED STATES: Virginia: Great Falls 12.IX. Collection N. Banks

barbatus Osten Sacken, **Anastoechus** LECTOTYPE ♂ 12719
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 252-53 pin
UNITED STATES: Wyoming: Cheyenne 21.VIII. O. Sacken
Lectotype designated by Hall *in* Hall and Evenhuis (1981: 153-54).

bifurca Loew, **Exoprosopa** HOLOTYPE ♀ 12636
1869 *Berliner Entomol. Z.* **13:** 15-16 pin
UNITED STATES: California: [no further data] Agassiz

Loew's description of *bifurca* was apparently based on a single specimen because there is no range of measurements recorded. There are two female specimens in the MCZ labeled as types. The one in the best condition is considered to be the holotype. It fits Loew's description and measurements and carries a label "bifurca m." in Loew's handwriting. The other specimen is denuded, smaller than the holotype, and carries a label "bifurca" in Banks' handwriting. The latter specimen probably does not belong to the original type series.

bigradata Loew, **Anthrax** HOLOTYPE [♀] 12655
1869 *Berliner Entomol. Z.* **13:** 23-24 pin
CUBA: [no further data] Gundlach

Original description incorrectly cites sex of type as "♂".

borealis Johnson, **Phthiria** HOLOTYPE ♀ 27054
1910 *Psyche* **17:** 229 pin
UNITED STATES: Maine: Fort Kent 7.VIII. 1910
C.W. Johnson Collection
Present name: *Phthiria (Poecilognathus) borealis* Johnson

brevicornis Loew, **Sparnopolius** SYNTYPES 2 ♀ 12723
1872 *Berliner Entomol. Z.* **16:** 79 pin
UNITED STATES: Texas: [no further data] Belfrage

Though Loew gives no range of measurements, two specimens are labeled as types in the MCZ. They are left here as syntypes until their type status can be clarified.

cachinnans Osten Sacken, **Bombylius** LECTOTYPE ♂ 12693
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 250 pin
UNITED STATES: California: Sonoma County 2.IV.-9.V.
R. Osten Sacken

Male and female on same pin. Lectotype designated by Evenhuis *in* Hall and Evenhuis (1980: 29).

calvus Loew, **Geron** SYNTYPES 2 ♀ 12711
1863 *Berliner Entomol. Z.* **7:** 303-04 pin
UNITED STATES: New York [no further data]

Loew's description does not include a range of measurements though two specimens are labeled as types in the MCZ. Until this discrepancy can be clarified, they are left as syntypes.

candidulus Loew, **Systoechus** LECTOTYPE ♂ 12716
1863 *Berliner Entomol. Z.* **7:** 302 pin
UNITED STATES: Wisconsin: [no further data] O. Sacken
Loew's description cites a range of measurements though only one male was located in the MCZ. The male is here designated *lectotype.*

canuta Hall, **Thevenemyia** HOLOTYPE ♂ 31339
1969 *Univ. Calif. Publ. Entomol.* pin
56: 28-29 Fig. 8
UNITED STATES: Arizona: Reef 10.X. C.W. Johnson Collection

capito Osten Sacken, **Pantarbes** LECTOTYPE ♂ 12720
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 256 pin
UNITED STATES: California: Sonoma County 2.IV.-9.V. R. Osten Sacken
Lectotype male designated herein by J.C. Hall.

cervinus Loew, **Aphoebantus** HOLOTYPE ♀ 12684
1872 *Berliner Entomol. Z.* **16:** 76-77 pin
UNITED STATES: Texas: [no further data] Belfrage

ceyx Loew, **Anthrax** LECTOTYPE ♂ 12664
1869 *Berliner Entomol. Z.* **13:** 19 pin
UNITED STATES: Virginia [no further data]
Loew's description cites a range of measurements though only one male was found in the MCZ. It is here designated *lectotype.*
Present name: *Poecilanthrax demogorgon* (Walker)

contigua Loew, **Argyromoeba** HOLOTYPE ♀ 12679
1869 *Berliner Entomol. Z.* **13:** 30-31 pin
UNITED STATES: Virginia: [no further data] Loew
Present name: *Anthrax argyropygus argyropygus* Wiedemann

coquilletti Johnson, **Phthiria** SYNTYPES 2 ♂, 4 ♀ 7554
1902 *Can. Entomol.* **34:** 240-41 pin
UNITED STATES: New Jersey: 1 ♂, 4 ♀, Riverton 4.VII.1891; 1 ♂, Jamesburg 4.VII.1891 C.W. Johnson Collection

Three syntypes are in USNM; one syntype is in SNOW; these specimens are left as syntypes pending generic revision.

Present name: *Phthiria (Poecilognathus) coquilletti* Johnson

cubana Loew, **Exoprosopa** SYNTYPES 1 ♂, 1 ♀ 12641
1869 *Berliner Entomol. Z.* **13:** 14-15 pin
CUBA: [no further data] Gundlach

Two syntypes are also located in ZMHU. These specimens are left as syntypes pending generic revision.

curta Loew, **Anthrax** HOLOTYPE ♂ 12654
1869 *Berliner Entomol. Z.* **13:** 22 pin
UNITED STATES: California: [no further data] Agassiz
Present name: *Hemipenthes curta* (Loew)

cyanoceps Johnson, **Phthiria** HOLOTYPE ♂ 27053
1903 *Psyche* **10:** 184 pin
UNITED STATES: Massachusetts: Cohasset 8.IX.
C.W. Johnson Collection
Present name: *Phthiria (Poecilognathus) cyanoceps* Johnson

decora Loew, **Exoprosopa** HOLOTYPE ♀ 12630
1869 *Berliner Entomol. Z.* **13:** 13 pin
UNITED STATES: Wisconsin: [no further data] Kennicot

delila Loew, **Argyromoeba** HOLOTYPE ♀ 12674
1869 *Berliner Entomol. Z.* **13:** 28 pin
UNITED STATES: California: [no further data] Agassiz
Present name: *Anthrax delila* (Loew)

diagonalis Loew, **Anthrax** HOLOTYPE ♀ 12656
1869 *Berliner Entomol. Z.* **13:** 21 pin
UNITED STATES: California: [no further data] Agassiz
Present name: *Paravilla diagonalis* (Loew)

dodrans Osten Sacken, **Exoprosopa** SYNTYPES 2 ♂ 12634
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 234-35 pin
UNITED STATES: [Colorado]: Colorado Springs [no date]
O. Sacken

These specimens are left here as syntypes pending generic revision.

dorcadion Osten Sacken, **Exoprosopa** LECTOTYPE ♀ 12631
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 231-33 pin
UNITED STATES: Maine [no further data]

Osten Sacken's original description of *dorcadion* is based on syntypes from "Summit Station, Central Pacific Railroad, California (July 17); Webber Lake, Sierra Nevada, California (July 26); Shasta district, California (H. Edwards); Washington Territory (the same); Georgetown, Colorado (August 12); Twin Lake Creek, Colorado (W.L. Carpenter); White Mountains, New Hampshire (H.K. Morrison); Maine — 2 specimens from Denver, Colorado (Uhler)." The MCZ has all but the New Hampshire and Shasta district specimens. The Summit Station specimen also carries the label "Sierra Nevada." All the specimens are females except for the one male from Denver, Colorado. The female specimen from Maine is in the best condition and is here designated *lectotype*. Three syntypes are also deposited in AMNH.

doris Osten Sacken, **Exoprosopa** SYNTYPE ♀ 12632
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 235-36 pin
UNITED STATES: Nevada: Humboldt Station 29.VII. O. Sacken

One syntype (headless) is deposited in AMNH. These specimens are left as syntypes pending generic revision.

edwardsii Loew, **Allocotus** HOLOTYPE [♂] 12704
1872 *Berliner Entomol. Z.* **16:** 81-82 pin
UNITED STATES: California: [no further data] H. Edwards

Original description incorrectly states sex as "♀".

Present name: *Paracosmus edwardsii* (Loew)

egerminans Loew, **Phthiria** LECTOTYPE [♀] 12708
1872 *Berliner Entomol. Z.* **16:** 80-81 pin
UNITED STATES: California: [no further data] H. Edwards

Original description incorrectly cites sex of type as "♂". Loew's description cites a range of measurements though only one female was found in the MCZ. It is here designated *lectotype*.

eremita Osten Sacken, **Exoprosopa** HOLOTYPE ♂ 12637
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 236 pin
UNITED STATES: California: Shasta District [15.VII.] H. Edwards

euplanes Loew, **Argyromoeba** HOLOTYPE ♀ 12681
1869 *Berliner Entomol. Z.* **13:** 30 pin
CUBA: [no further data] Gundlach
Present name: *Anthrax euplanes* (Loew)

fenestrata Osten Sacken, **Ploas** LECTOTYPE ♀ 12702
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 260-61 pin
UNITED STATES: California: San Raphael 12.IV. O. Sacken
Osten Sacken based his description of *fenestrata* on two males and one female. Of these syntypes, the best preserved (the female) is here designated *lectotype.*
Present name: *Conophorus fenestratus* (Osten Sacken)

flaviceps Loew, **Anthrax** LECTOTYPE ♀ 12663
1869 *Berliner Entomol. Z.* **13:** 18-19 pin
MEXICO: Tamaulipas [no further data]
Of the two female syntypes of this species in the MCZ, the best preserved is here designated *lectotype.*
Present name: *Poecilanthrax flaviceps* (Loew)

fraudulentus Johnson, **Bombylius** HOLOTYPE ♂ 7552
1907 *Psyche* **14:** 99-100 pin
UNITED STATES: Massachusetts: Provincetown 27.VI.1904
C.W. Johnson Collection

fuliginosa Loew, **Anthrax** HOLOTYPE ♂ 12661
1869 *Berliner Entomol. Z.* **13:** 20 pin
UNITED STATES: California [no further data]
Specimen rubbed.
Present name: *Poecilanthrax fuliginosus* (Loew)

fur Osten Sacken, **Argyromoeba** LECTOTYPE ♂ 12678
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 244-45 pin
UNITED STATES: Texas: Dallas [no date] Boll
Osten Sacken based his description of *fur* on one male and two female syntypes. The best preserved of these (the male) is here designated *lectotype.*
Present name: *Anthrax limatulus fur* (Osten Sacken)

gazophylax Loew, **Exoprosopa** HOLOTYPE ♀ 12629

1869 *Berliner Entomol. Z.* **13:** 12-13 pin
UNITED STATES: California: [no further data] Agassiz
Head missing.
Present name: *Ligyra gazophylax* (Loew)

gibbus Loew, **Lordotus** HOLOTYPE ♀ 12724
1863 *Berliner Entomol. Z.* **7:** 303 pin
MEXICO: [Tamaulipas]: Matamoros [no further data]
The label data cites the locality as "Matamoras."

haemorrhoicus Loew, **Bombylius** HOLOTYPE ♂ 12696
1863 *Berliner Entomol. Z.* **7:** 300 pin
CUBA: [no further data] [Gundlach]
Original description cites collector as "Riehl," label data cites "Gundlach."
Present name: *Heterostylum haemorrhoicum* (Loew)

harrisi Osten Sacken, **Epibates** HOLOTYPE ♂ 26400
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 273 pin
[No locality label] H. Gray
Hall (1969: 38) proposed a lectotype male (MCZ Type No. 31340) and allolectotype female for *harrisi* under the assumption that the original type specimen was lost.[1] The type male is, in fact, present in the T.W. Harris Collection [in MCZ] as described by Osten Sacken.
Present name: *Thevenemyia harrisi* (Osten Sacken)

humilis Osten Sacken, **Phthiria** HOLOTYPE ♂ 12710
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 264 pin
UNITED STATES: California: Sonoma County 4.VII.
O. Sacken

incanus Johnson, **Bombylius** HOLOTYPE ♂ 7553
1907 *Psyche* **14:** 97-98 pin
UNITED STATES: Massachusetts: Provincetown 2.VI.1904
C.W. Johnson Collection
Present name: *Bombylius (Zephyrectes) incanus* Johnson

[1]Though neotypes should be proposed for lost or destroyed types, Hall mistakingly proposed a lectotype and allolectotype which, therefore, have no validity nomenclatorially.

johnsoni Painter, **Geron** HOLOTYPE ♂ 27266
1932 *Trans. Am. Entomol. Soc.* **58:** 155 pin
UNITED STATES: Massachusetts: Horseneck Beach 30. VII.1913 C.W. Johnson Collection

lancifer Osten Sacken, **Bombylius** LECTOTYPE ♂ 12692
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 251 pin
UNITED STATES: California: [no further data] Sacken
Lectotype male designated by Evenhuis *in* Hall and Evenhuis (1980: 57).

lepidotoides Johnson, **Chrysanthrax** HOLOTYPE ♂ 7550
1919 *Psyche* **26:** 12 pin
UNITED STATES: New Jersey: Iona 16.VI.1902 C.W. Johnson Collection

limbata Loew, **Ploas** LECTOTYPE ♀ 12700
1869 *Berliner Entomol. Z.* **13:** 31 pin
UNITED STATES: New Mexico [no further data]
Specimen badly rubbed; right wing glued to point below specimen; head, left wing, left fore- and hind- and right mid- and hindlegs beyond coxae missing. Loew's description cites a range of measurements though only one female was found in the MCZ. It is here designated *lectotype.*
Present name: *Conophorus limbatus* (Loew)

luctifer Osten Sacken, **Epibates** HOLOTYPE ♂ 12728
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 271-72 pin
[CANADA: British Columbia]: Vancouver Island [no date] G.R. Crotch
Present name: *Thevenemyia luctifera* (Osten Sacken)

macer Loew, **Systropus** LECTOTYPE ♀ 12726
1863 *Berliner Entomol. Z.* **7:** 305 pin
UNITED STATES: Pennsylvania [no further data]
Of the three syntypes of *macer* (1 male, 2 females) in the MCZ, the best preserved of these (a female) is here designated *lectotype.*

macropterus Loew, **Geron** HOLOTYPE ♂ 12712

1869 *Berliner Entomol. Z.* **13:** 172-73 pin
UNITED STATES: New York: Geneseo [no further data]
Head and thorax damaged; abdomen beyond third segment missing.
Present name: *Geron (Empidigeron) calvus* Loew

magnus Osten Sacken, **Epibates** HOLOTYPE ♀ 12731
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 272-73 pin
[CANADA: British Columbia]: Vancouver Island [no date] G.R. Crotch
Present name: *Thevenemyia magna* (Osten Sacken)

marginatus Osten Sacken, **Epibates** HOLOTYPE ♀ 12730
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 272 pin
UNITED STATES: California: San Francisco [no date] H. Edwards
Present name: *Thevenemyia marginata* (Osten Sacken)

metopium Osten Sacken, **Bombylius** HOLOTYPE ♂ 12690
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 249 pin
UNITED STATES: California: [San Francisco] 19.IV O. Sacken

modestus Loew, **Leptochilus** SYNTYPES 1 ♂, 1 ♀ 12685
1872 *Berliner Entomol. Z.* **16:** 77-78 pin
UNITED STATES: Texas: [no further data] Belfrage
The specimens are left here as syntypes pending revision of the genus.
Present name: *Epacmus modestus* (Loew)

molitor Loew, **Anthrax** HOLOTYPE ♀ 12652
1869 *Berliner Entomol. Z.* **13:** 26-27 pin
UNITED STATES: California: [no further data] Agassiz
Head glued to thorax.
Present name: *Villa molitor* (Loew)

mucorea Loew, **Anthrax** HOLOTYPE ♀ 12651

1869 *Berliner Entomol. Z.* **13:** 27 pin
UNITED STATES: Nebraska: [no further data] [F.V. Hayden]
Collector recorded in Osten Sacken (1903: 95).
Present name: *Villa mucorea* (Loew)

muricatus Osten Sacken, **Epibates** HOLOTYPE ♂ 12729
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 272 pin
UNITED STATES: California: Sierra Nevada [no date] H. Edwards
Present name: *Thevenemyia muricata* (Osten Sacken)

mus Osten Sacken, **Triodites** LECTOTYPE ♂ 12683
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 246-47 pin
UNITED STATES: Utah: Salt Lake City 1.VIII. O. Sacken
Of the three syntypes of *mus* (1 male, 2 females) located in the MCZ, the best preserved of these (the male) is here selected as *lectotype*.
Present name: *Aphoebantus mus mus* (Osten Sacken)

nigricauda Loew, **Anthrax** HOLOTYPE ♀ 12650
1869 *Berliner Entomol. Z.* **13:** 24 pin
UNITED STATES: Massachusetts: [no further data] Scudder
Head missing.
Present name: *Villa fulviana nigricauda* (Loew)

nigripennis Loew, **Ploas** LECTOTYPE ♀ 12697
1872 *Berliner Entomol. Z.* **16:** 80 pin
UNITED STATES: California: [no further data] H. Edwards
Loew's description cites a range of measurements though only one female was found in the MCZ. It is here designated *lectotype*.
Present name: *Conophorus nigripennis* (Loew)

notata Loew, **Phthiria** HOLOTYPE ♀ 12706
1863 *Berliner Entomol. Z.* **7:** 113-14 pin
UNITED STATES: California: [no further data] Agassiz
Present name: *Phthiria (Poecilognathus) loewi* Painter

nubifera Loew, **Exoprosopa** LECTOTYPE ♂ 12639
1869 *Berliner Entomol. Z.* **13:** 16 pin

CUBA: [no further data] [Poey]

Original description cites collector as "Gundlach," label data cites "Poey." Loew's description cites a range of measurements though only one male was found in the MCZ. The male is here designated *lectotype*.

obesula Loew, **Ploas** SYNTYPES 3 ♂ 12699
1872 *Berliner Entomol. Z.* **16:** 80 pin
UNITED STATES: California: [no further data] H. Edwards

Loew's original description of *obesula* was based on an unstated number of males and females. Only three males were found in the MCZ. They are left here as syntypes until the genus is revised.

Present name: *Conophorus obesulus* (Loew)

obsoleta Loew, **Argyromoeba** HOLOTYPE [♀] 12675
1869 *Berliner Entomol. Z.* **13:** 29 pin
UNITED STATES: Missouri [no further data]

Original description incorrectly states sex of type as "♂".

Present name: *Anthrax limatulus limatulus* Say

occidentalis Johnson, **Spogostylum** SYNTYPES 2 ♀ 7547
1913 *Bull. Am. Mus. Nat. Hist.* pin
32: 56
UNITED STATES: 1 ♀, Colorado: Denver 5.VIII.1897; 1 ♀, Washington: Seattle [no further data] C.W. Johnson Collection

These specimens are left here as syntypes pending generic revision.

Present name: *Anthrax analis* Say

oreas Osten Sacken, **Systoechus** LECTOTYPE ♂ 12718
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 254 pin
UNITED STATES: California: Webber Lake 22.VII. O. Sacken

Lectotype designated by Hall *in* Hall and Evenhuis (1981: 147).

palliata Loew, **Anthrax** HOLOTYPE ♀ 12657
1869 *Berliner Entomol. Z.* **13:** 20-21 pin
UNITED STATES: Illinois: [no further data] Osten Sacken

Present name: *Paravilla palliata* (Loew)

parva Loew, **Exoprosopa** LECTOTYPE ♂ 12640
1869 *Berliner Entomol. Z.* **13:** 17 pin
CUBA: [no further data] Gundlach
Though Loew's description cites a range of measurements, only one male was located in the MCZ. It is here designated *lectotype.*
Present name: *Neodiplocampta (Neodiplocampta) parva* (Loew)

parvicornis Loew, **Anthrax** HOLOTYPE ♂ 12658
1869 *Berliner Entomol. Z.* **13:** 23 pin
UNITED STATES: Illinois: [Chicago] [no date] Osten Sacken
Present name: *Rhynchanthrax parvicornis* (Loew)

pauper Loew, **Argyromoeba** HOLOTYPE ♀ 12677
1869 *Berliner Entomol. Z.* **13:** 29-30 pin
UNITED STATES: Illinois [no further data]
Present name: *Anthrax pauper* (Loew)

pertusa Loew, **Anthrax** HOLOTYPE ♂ 12659
1869 *Berliner Entomol. Z.* **13:** 18 pin
UNITED STATES: New Mexico: [10.IV.] [no further data]
Present name: *Thyridanthrax pertusa* (Loew)

planus Osten Sacken, **Lordotus** HOLOTYPE ♂ 12725
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 258-59 pin
UNITED STATES: California: Marin County [no date] O. Sacken

proboscidea Loew, **Anthrax** HOLOTYPE ♂ 12653
1869 *Berliner Entomol. Z.* **13:** 17-18 pin
MEXICO: Sonora: [no further data] Schott
Present name: *Lepidanthrax proboscideus* (Loew)

pulchellus Loew, **Bombylius** LECTOTYPE ♂ 12687
1863 *Berliner Entomol. Z.* **7:** 300 pin
UNITED STATES: Illinois [no further data]
Lectotype designated by Evenhuis *in* Hall and Evenhuis (1980:79).

quinquenotata Johnson, **Phthiria** HOLOTYPE ♀ 7556

1903 *Psyche* **10:** 185 pin
UNITED STATES: Colorado: Grand Junction 25.V.1900 C.W. Johnson Collection
Present name: *Oligodranes quinquenotata* (Johnson)

ravus Loew, **Bombylius** HOLOTYPE ♀ 12694
1863 *Berliner Entomol. Z.* **7:** 301-02 pin
MEXICO [no further data]
Present name: *Bombylius (Zephyrectes) ravus* Loew

rufula Osten Sacken, **Ploas** LECTOTYPE ♂ 12701
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 261 pin
UNITED STATES: California: San Geronimo 19.IV. O. Sacken
Present name: *Conophorus rufulus* (Osten Sacken)

sagata Loew, **Anthrax** LECTOTYPE ♂ 12671
1869 *Berliner Entomol. Z.* **13:** 21-22 pin
MEXICO: [Tamaulipas]: Matamoros [no further data]
Head missing; label data cites locality as "Matamor*as*". Loew's description cites a range of measurements, though only one male was found in the MCZ. It is designated here as *lectotype.*
Present name: *Hemipenthes sagata* (Loew)

scolopax Osten Sacken, **Phthiria** SYNTYPES [2♂, 1♀] 12789
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 263-64 pin
UNITED STATES: Colorado: Manitou 17-18.VIII. O. Sacken
The original description of *scolopax* was based on one male and three females. Two male and one female syntypes are located in the MCZ. These specimens are left here as syntypes pending generic revision.
Present name: *Phthiria (Poecilognathus) scolopax* Osten Sacken

scrobiculata Loew, **Anthrax** LECTOTYPE ♂ 12648
1869 *Berliner Entomol. Z.* **13:** 24-25 pin
UNITED STATES: Illinois [no further data]
Of the two male syntypes of *scrobiculata* in the MCZ, the best of these is here designated *lectotype.*
Present name: *Villa scrobiculata* (Loew)

seminigra Loew, **Hemipenthes** HOLOTYPE [♂] 12673
1869 *Berliner Entomol. Z.* **13:** 27-28 pin
CANADA: Saskatchewan: [no further data] Kennicot
Head missing; original description incorrectly cites sex of type as "♀"
Present name: *Hemipenthes seminigra* Loew

semirufus Loew, **Bombylius** LECTOTYPE ♂ 12695
1872 *Berliner Entomol. Z.* **16:** 78 pin
HAITI: [Gérémie]: [no date] P.R. Uhler
The location of Gérémie is cited from the label data. It was omitted from the original description. Of the two syntypes of *semirufus* (one male, one female) in the MCZ, the best preserved (the male) is here designated *lectotype.*
Present name: Heterostylum semirufum (Loew)

serpentina Osten Sacken, **Dipalta** LECTOTYPE ♀ 12646
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 237 pin
UNITED STATES: California: Mt. Shasta District [no date] O. Sacken
Osten Sacken based his description of *serpentina* on one male and two female syntypes. The best preserved of these (a female) is here designated *lectotype.*

shawii Johnson, **Anthrax** HOLOTYPE♂ 7549
1908 *Psyche* **15:** 14-15 pin
UNITED STATES: New Hampshire: Hampton 27.VIII. 1906 S.A. Snow
The holotype also carries a type label reading "holotype no. 599".[1]
Present name: *Villa shawii* (Johnson)

sima Osten Sacken, **Exoprosopa** LECTOTYPE [♂] 12628
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 231-33 pin
UNITED STATES: Nevada: Humboldt Station: Central Pacific Railroad [no further data]
Osten Sacken's original description of *sima* incorrectly cites the sex of the three syntypes as female. They are, in fact, all males. The best preserved is here designated *lectotype.*

---

[1]This number probably pertains to Johnson's personal collection prior to MCZ accession (Woodley, personal communication).

slossonae Johnson, **Spogostylum** HOLOTYPE ♂ 7546
1913 *Bull. Am. Mus. Nat. Hist.* **32:** 55 pin
UNITED STATES: Kentucky: Cumberland Gap VII.1876 G. Dimmock
Present name: *Anthrax aterrimus* (Bigot)

sordida Loew, **Exoprosopa** SYNTYPES [2♀] 12642
1869 *Berliner Entomol. Z.* **13:** 14 pin
MEXICO: 1 ♀, Tamaulipas: [no further data]; 1♀, [Tamaulipas]: Matamoros [no further data]
Loew's original description of *sordida* cites an unspecified number of males and females. Only two males were found in the MCZ; label data cites locality of the latter syntype as "Matamor*as*." These specimens are left here as syntypes pending generic revision.

stellans Loew, **Argyromoeba** HOLOTYPE [♀] 12676
1869 *Berliner Entomol. Z.* **13:** 28-29 pin
UNITED STATES: Oregon [no further data]
Right wing broken; original description incorrectly cites sex of type as "♂".
Present name: *Anthrax stellans* (Loew)

stenozona Loew, **Anthrax** LECTOTYPE ♀ 12649
1869 *Berliner Entomol. Z.* **13:** 25 pin
UNITED STATES: Illinois [no further data]
A *lectotype* is here designated for the one female in MCZ as Loew's description cites a range of measurements, implying a series of specimens.
Present name: *Villa stenozona* (Loew)

subauratus Loew, **Geron** SYNTYPES 2 ♂, 1 ♀ 12714
1863 *Berliner Entomol. Z.* **7:** 304-05 pin
UNITED STATES: Pennsylvania: [no further data] Osten Sacken
The specimens are left here as syntypes until the genus is revised.

subvarius Johnson, **Bombylius** LECTOTYPE ♀ 7551
1907 *Psyche* **14:** 98-99 pin
UNITED STATES: Pennsylvania: Lehigh Gap 26.VI.1901 H.L. Viereck
Lectotype female designated herein.
Present name: *Bombylius atriceps* Loew

sulphurea Loew, **Phthiria** HOLOTYPE ♀ 12705
1863 *Berliner Entomol. Z.* **7:** 113 pin
UNITED STATES: New Jersey: [no further data] Glover
Present name: *Phthiria (Poecilognathus) sulphurea* Loew

titubans Osten Sacken, **Exoprosopa** HOLOTYPE [♂] 12633
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 233-34 pin
UNITED STATES: [Colorado]: Denver [no date] O. Sacken
Original description incorrectly states sex of type as "♀".

trabalis Loew, **Exoprosopa** HOLOTYPE ♀ 12638
1869 *Berliner Entomol. Z.* **13:** 13-14 pin
MEXICO: [Veracruz]: Jalapa [no further data]
Present name: *Exoprosopa anthracoidea* Jaennicke

validus Loew, **Bombylius** LECTOTYPE ♂ 12689
1863 *Berliner Entomol. Z.* **7:** 300 - pin
UNITED STATES: Virginia: [no further data] Osten Sacken
Lectotype designated by Evenhuis *in* Hall and Evenhuis (1980: 90).

virgata Osten Sacken, **Toxophora** SYNTYPES 1 ♂, 1 ♀ 12727
1877 *Bull. U.S. Geol. Geogr. Surv. Terr.* **3:** 266-67 pin
UNITED STATES: Georgia [no further data]
Osten Sacken based his description of *virgata* on two males and two females from Georgia and Texas. A male and a female from Georgia are in the MCZ. The Texas specimens have not been located. These specimens are left here as syntypes pending generic revision.

vitripennis Loew, **Geron** SYNTYPES 2 ♂ 12713
1869 *Berliner Entomol. Z.* **13:** 173 pin
UNITED STATES: "Middle States" [no further data]
No locality labels on type specimens. Until the genus is revised they are left as syntypes.

vulgaris Loew, **Systoechus** LECTOTYPE ♂ 12717
1863 *Berliner Entomol. Z.* **7:** 302-03 pin
UNITED STATES: Nebraska: [no further data] [F.V. Hayden]
Lectotype designated by Hall *in* Hall and Evenhuis (1981: 151); original description incorrectly states collector as "Osten Sacken." Osten Sacken (1903: 95) gives the correct collector.

webberi Johnson, **Villa** HOLOTYPE ♂ 12680
1919 *Psyche* **26:** 11 pin
UNITED STATES: Massachusetts: Lunenberg 3.VI.1914 [no collector]
Present name: *Hemipenthes webberi* (Johnson)

willistoni Osten Sacken, **Pantarbes** HOLOTYPE ♂ 12722
1887 *Biologia Centrali-Americana* pin
1: 153
UNITED STATES: Arizona: [no further data] O. Sacken

xanthomeros Marston, **Anthrax** HOLOTYPE ♀ 32555
1970 *Smithson. Contrib. Zool.* pin
43: 52-53 Pl. 3g
BRITISH HONDURAS: Benque Viejo [no date] Father Stanton

GENUS-GROUP INVENTORY
(indexed by present combination)

Anastoechus: barbatus
Anthrax: bigradata, contigua, delila, euplanes, fur, obsoleta, occidentalis, pauper, slossonae, stellans, xanthomeros
Aphoebantus: cervinus, mus mus
Bombylius (Bombylius): albicapillus, atriceps, aurifer, cachinnans, fraudulentus, lancifer, metopium, pulchellus, subvarius, validus
Bombylius (Zephyrectes): incanus, ravus
Chrysanthrax: lepidotoides
Conophorus: amabilis, atratulus, fenestratus, limbatus, nigripennis, obesulus, rufulus
Dipalta: banksi, serpentina
Epacmus: modestus
Exoprosopa: agassizi, bifurca, cubana, decora, dodrans, dorcadion, doris, eremita, nubifera, sima, sordida, titubens, trabalis
Geron: albidipennis, calvus, johnsoni, macropterus, subauratus, vitripennis
Hemipenthes: curta, sagata, seminigra, webberi
Heterostylum: haemorrhoicum, semirufum
Lepidanthrax: proboscideus

Ligyra: gazophylax
Lordotus: gibbus, planus
Neodiplocampta (Neodiplocampta): parva
Oligodranes: quinquenotata
Pantarbes: capito, willistoni
Paravilla: diagonalis, palliata
Paracosmus: edwardsii
Phthiria (Phthiria): egerminans, humilis
Phthiria (Poecilognathus): aldrichi, borealis, coquilletti, cyanoceps, loewi, scolopax, sulphurea
Poecilanthrax: alpha, ceyx, flaviceps, fuliginosus
Rhynchanthrax: parvicornis
Sparnopolius: brevicornis
Systoechus: candidulus, oreas, vulgaris
Systropus: arizonicus, macer
Thevenemyia: canuta, harrisi, luctifera, magna, marginata
Thyridanthrax: pertusa
Toxophora: virgata
Villa: adjusta, lateralis arenicola, molitor, mucorea, fulviana nigricauda, scrobiculata, shawii, stenozona

ACKNOWLEDGMENTS

I wish to thank Mr. Jack C. Hall for reviewing the manuscript of this paper and Drs. Pedro Wygodzinsky of the American Museum of Natural History and H. Schumann of the Museum für Naturkunde der Humboldt-Universität, Berlin for their help in locating Osten Sacken and Loew types, respectively, in their museums. I also wish to express my sincere gratitude to Mr. Norman E. Woodley for his assistance during my visit to the MCZ and for his comments and suggestions concerning the manuscript of this study. I thank Ms. Margaret K. Thayer for her help in obtaining for me the initial loans of some of the type material in the MCZ.

Travel for this study was supported by National Science Foundation Grant DEB 79-10192 to the University of California, Riverside.

LITERATURE CITED

Banks, N. 1909. A new species of *Systropus* (Bombyliidae). Entomol. News, **20:** 18.

Cole, F.R. 1917. Notes on Osten Sacken's group "Poecilanthrax," with descriptions of new species. J. N.Y. Entomol. Soc., **25:** 67-80.

Hall, J.C. 1969. A review of the subfamily Cylleniinae with a world revision of the genus *Thevenemyia* Bigot (*Eclimus* auct.) (Diptera: Bombyliidae). Univ. Calif. Publ. Entomol., **56:** 1-85.

Hall, J.C., and N.L. Evenhuis. 1980. Part 13, Number 1. Family Bombyliidae, pp. 1-96. *In* Griffiths, G.C.D. (ed.), Flies of the Nearctic Region. Vol. V. Stuttgart, E. Schweizerbart'sche.

_____. 1981. Part 13, Number 2. Family Bombyliidae, pp. 97-184. *In* Griffiths, G.C.D. (ed.), Flies of the Nearctic Region. Vol. V. Stuttgart, E. Schweizerbart'sche.

Johnson, C.W. 1902. New North American Diptera. Can. Entomol., **34:** 240-42.

_____. 1903. Descriptions of three new Diptera of the genus *Phthiria.* Psyche, **10:** 184-85.

_____. 1907. A review of the species of the genus *Bombylius* of the eastern United States. Psyche, **14:** 95-100.

_____. 1908. Notes on New England Bombyliidae, with a description of a new species of *Anthrax.* Psyche, **15:** 14-15.

_____. 1910. Some additions of the dipteran fauna of New England. Psyche, **17:** 228-35.

_____. 1913. Insects of Florida. I. Diptera. Bull. Amer. Mus. Nat. Hist., **32:** 37-90.

_____. 1919. New species of the genus *Villa (Anthrax).* Psyche, **26:** 11-13.

_____. 1921. New species of Diptera. Occas. Pap. Boston Soc. Nat. Hist., **38:** 57-99.

Loew, H. 1863a. Diptera Americae septentrionalis indigena. Centuria tertia. Berliner Entomol. Z., **7:** 1-55.

_____. 1863b. Diptera Americae septentrionalis indigena. Centuria quarta. Berliner Entomol. Z., **7:** 275-326.

_____. 1869a. Diptera Americae septentrionalis indigena. Centura octava. Berliner Entomol. Z., **13:** 1-52.

_____. 1869b. Diptera Americae septentrionalis indigena. Centuria nona. Berliner Entomol. Z., **13:** 129-186.

_____. 1872. Diptera Americae septentrionalis indigena. Centuria decima. Berliner Entomol. Z., **16:** 49-115.

Marston, N. 1970. Revision of New World species of *Anthrax* (Diptera: Bombyliidae) other than the *Anthrax albofasciatus* group. Smithson. Contrib. Zool., **43:** 1-148.

Osten Sacken, C.R. 1877a. Art. XIII. Western Diptera: Descriptions of new genera and species of Diptera from the region west of the Mississippi and especially from California. Bull. U.S. Geol. Geogr. Surv. Terr., **3:** 189-354.

_____. 1887b. Diptera. pp. 129-216. *In* Godman, F.D. and O. Salvin (eds.), Biologia Centrali-Americana. Zoologia-Insecta-Diptera. Vol. I. London, Taylor & Francis, 378 pp.

_____. 1903. Record of my life work in entomology. Cambridge, Mass., University Press, John Wilson & Sons, 204 pp.

Painter, R.H. 1932. A monographic study of the genus *Geron* Meigen as it occurs in the United States (Diptera: Bombyliidae). Trans. Amer. Entomol. Soc., **58:** 139-67.

Painter, R.H., and E.M. Painter. 1962. Notes on and redescriptions of types of North American Bombyliidae (Diptera) in European Museums. J. Kans. Entomol. Soc., **35:** 1-164.

Radovsky, F.J., G.A. Samuelson, and W.A. Steffan. 1976. Catalog of entomological types in the Bishop Museum. Introduction. Pac. Insects, **17:** 1-5.

...U.S. COMP. ZOOL.
LIBRARY
MAR 18 1985
HARVARD
UNIVERSITY

B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 30 JUNE 1982 NUMBER 470

SYSTEMATIC IMPLICATIONS OF INNERVATION PATTERNS IN TELEOST MYOTOMES

QUENTIN BONE[1] AND R. DANA ONO[2]

ABSTRACT. The peripheral innervation patterns of the red and white myotomal muscles from over 230 species representing more than 125 families of teleosts were studied. A distributed, multiple innervation pattern of teleost red superficial myotomal muscles was found without exception in all groups examined. There is variability in the innervation patterns of the white myotomal muscles, however. A terminally innervated pattern seems to be present in the basal groups of teleosts, while a trend toward distributed innervation occurs in the Neoteleostei. Stomiiformes possess a rather different distributed pattern which we suggest is the early, transitional stage from terminal to distributed innervation patterns in teleosts. There appears to be a distinct functional difference in the distributed and terminal innervation patterns. The innervation of the white myotomal fibers should be considered a taxonomically useful character in elucidating familial relationships.

INTRODUCTION

In all fishes, there are two main muscle fiber types in the myotomes, usually readily visible to the naked eye when the fish is sectioned transversely. Small-diameter, well-vascularized red muscle fibers normally form a thin superficial layer covering the much more numerous, larger-diameter, poorly-vascularized white muscle fibers that make up the major portion of the myotome. In some fishes, but not in all, other myotomal fiber types are present. These minor myotomal components will not concern us here. In all fishes,

[1]The Laboratory, Citadel Hill, Plymouth PL1 2PB, Devon, England.
[2]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

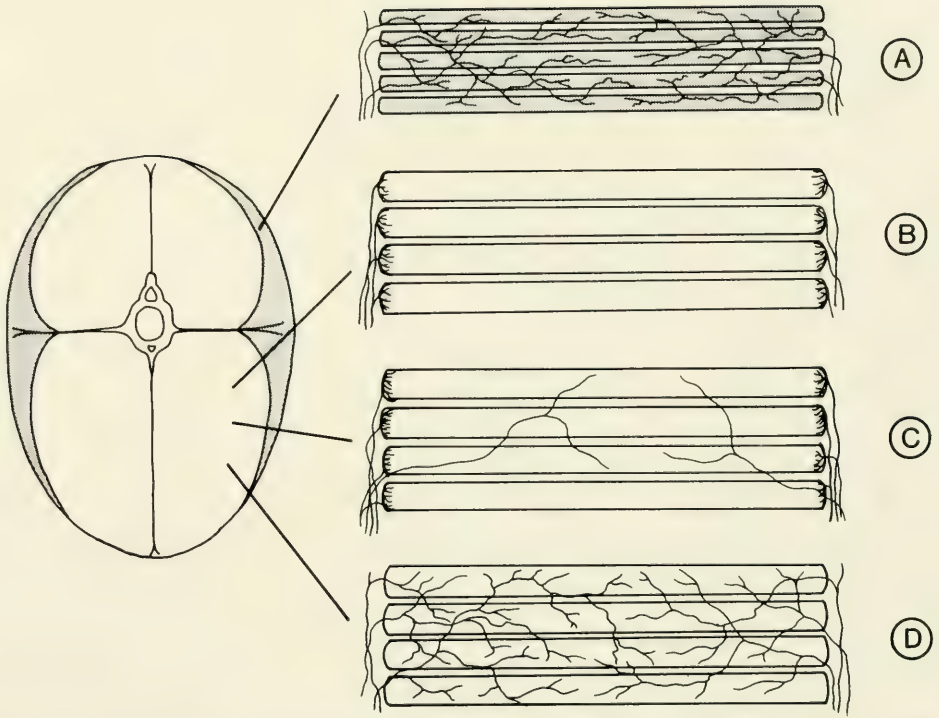


Figure 1. Cross section through hypothetical fish body depicting the larger white muscle mass and the superficial red muscle layer (stippled). A) distributed innervation of red muscle fibers; B) terminal innervation of white muscle fibers; C) terminal and small amount of distributed innervation of white muscle fibers in Stomiiformes; and D) distributed innervation of white muscle fibers.

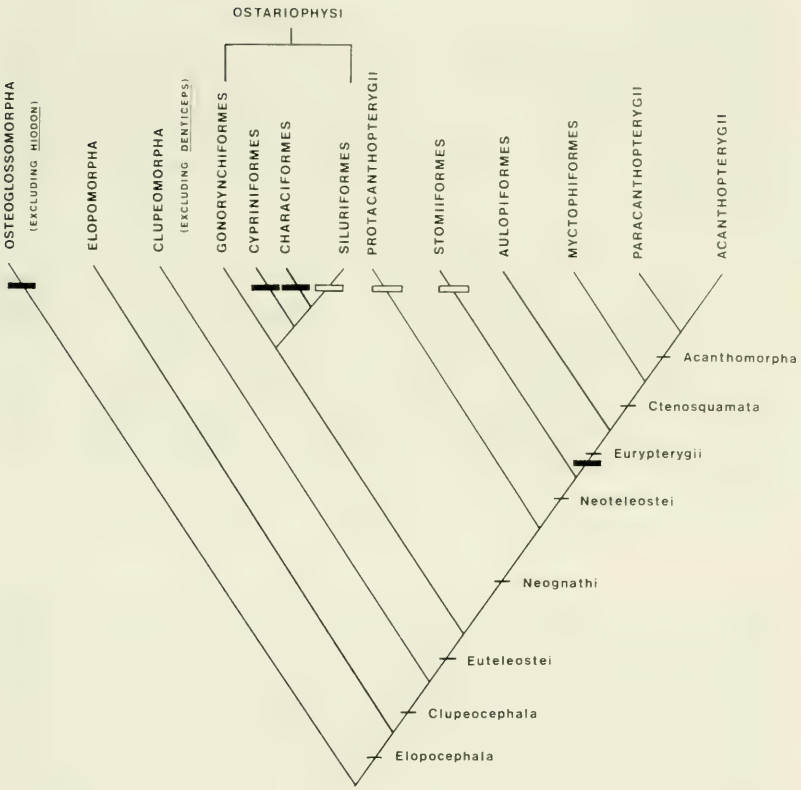


Figure 2. Hypothetical relationship of the Teleostei modified from Fink and Weitzman (1982) and Fink and Fink (1981) to show the extent of the distributed innervation pattern in teleosts. ▬ = distributed innervation in all. ▭ = distributed innervation in some members.

the red muscle fibers are multiply innervated in a distributed fashion, so that each muscle fiber receives a number of motor terminations along its length (Fig. 1A). In most teleosts, the white muscle fibers are similarly innervated (Figs. 1D, 3, 6), but in some an entirely different innervation pattern is found. In such fishes the white muscle fibers are innervated only at their myoseptal ends, so that innervation is focal and terminal (Figs. 1B, 4, 5).

Although this mode of innervation of white muscle fibers is rare in teleosts (Barets, 1961; Bone, 1964), investigations on other fish groups such as the Halecomorphi, Ginglymodi, Brachiopterygii,

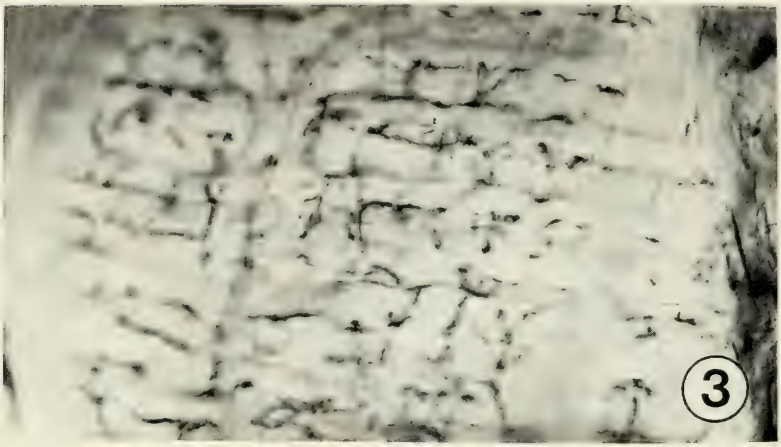


Figure 3. Distributed innervation pattern of motor endplates in white myotomal muscle fibers of *Morone labrax* as revealed by acetylcholinesterase (AChE) studies. (Mag. $\times 90$).

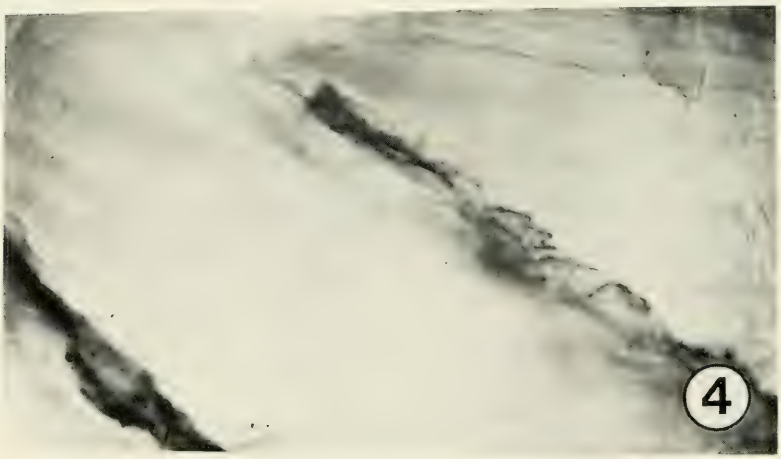


Figure 4. Terminal innervation pattern of motor endplates in white myotomal muscle fibers of the clupeomorph, *Sprattus sprattus*, as revealed by AChE studies. (Mag. $\times 90$).

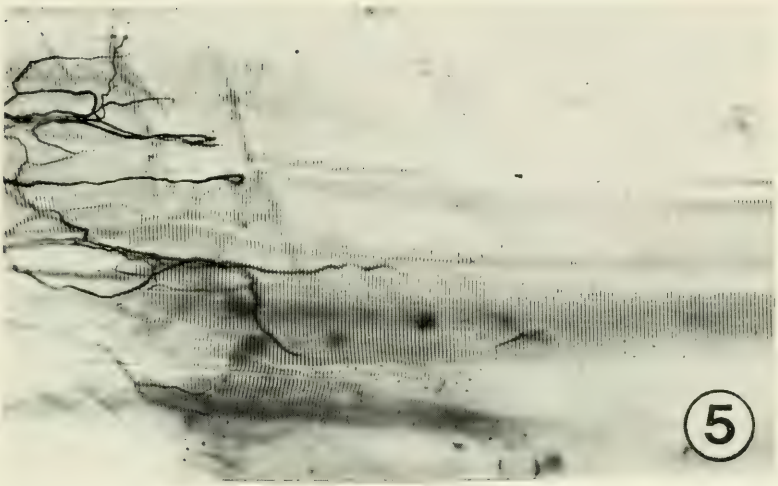


Figure 5. Silver impregnated axons of terminal innervation pattern in the white myotomal muscle fibers of the alepocephalid, *Xenodermichthys copei*. Winkelmann and Schmitt technique. (Mag. ×190).

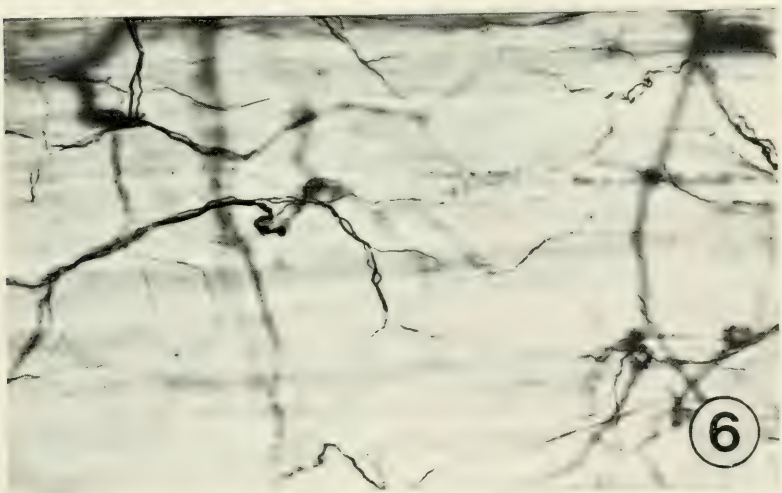


Figure 6. Silver impregnated axons of the distributed innervation pattern in the white myotomal muscle fibers of the gymnotid, *Eigenmannia virescens*. Winkelmann and Schmitt technique. (Mag. ×228).

Chondrostei (Acipenseridae, Polydontidae), hagfish, Elasmobranchiomorpha, and *Latimeria chalumnae* have shown that terminal innervation is universal in non-teleost groups (Bone, 1964 and unpublished; Ono, unpublished; Sakharov and Kashapova, 1979). In addition, terminal innervation is found in the Dipnoi, in the myotomal musculature of adult urodeles, and in urodele and anuran larvae (Best and Bone, 1973; Bone, unpublished; Ono, unpublished).

The wide distribution of the terminal innervation pattern of white muscle fibers led to a preliminary attempt (Bone, 1970) to link the occurrence of the terminal pattern in teleosts with the systematic position of the families in which it was found. This attempt was unsuccessful since relatively few families were examined. In this study, we report the results of a more detailed survey of the innervation pattern of white muscle fibers in different teleost groups that suggests that this character may be of interest to systematists.

MATERIALS AND METHODS

The innervation pattern of white muscle fibers was studied either by supravital staining with methylene blue in teleost Ringer solution, or by silver staining of 10% unbuffered formalin and Bouin-fixed material using the methods of Palmgren (1948) and Winkelmann and Schmitt (1957). During the last several years, we have collected marine fish material from the Caribbean, the Indian Ocean, the North Atlantic Ocean, and the Bay of Biscay. The freshwater fish material was collected by us from North American and European waters. In addition, we have been much assisted by other workers who have provided specially fixed or museum material from the waters of South America, Africa, Japan, New Zealand, and several deep-sea localities. We owe a particular debt of gratitude to Dr. P. H. Greenwood (BMNH) and to Mr. J. B. Badcock and Mr. N. Merrit (IOS) who have generously provided material from their collections.

TELEOST GROUPS AND THEIR INNVERVATION PATTERNS

The status of the different groups of teleosts is still subject to review, and different authors have adopted different systems of classification to indicate their views of the relationships of the

various groups. In this paper we have adopted the classification scheme of Rosen (1973) and Fink and Weitzman (1982). A complete checklist showing the teleosts examined is given in Table 1.

1) Osteoglossomorpha

Nine genera from this group were examined. With the exception of the two *Hiodon* species, all possess the distributed pattern of white muscle innervation.

2) Elopomorpha

We have examined 12 genera from this group representing the Elopiformes, Anguilliformes, and Notacanthiformes. All possess the terminal innervation pattern. Both the adults and leptocephali of *Elops* sp. and *Albula* sp. have the terminal pattern of white muscle innervation.

3) Clupeomorpha

Twenty-one species of clupeids belonging to 16 genera were studied. All possess the terminal innervation pattern with the sole exception of *Denticeps,* in which the white myotomal muscle has a distributed innervation.

4) Ostariophysi

We have examined 32 genera of ostariophysans representing the Gonorynchiformes, Characiformes, Cypriniformes, and Siluriformes. Some ostariophysans possess the terminal pattern (some siluroids and all gonorynchids), but the majority have the distributed pattern of innervation.

5) Protacanthopterygii

There is considerable uncertainty about the limits of this group, which has been reduced from its original size (Fink and Weitzman, 1982). The 16 species representing 14 genera listed in Table 1 are provisionally placed in this group.

6) Stomiiformes

Fifteen genera representing the two Infraorders Gonostomata and Photichthya (Weitzman, 1974) were studied. Two innervation patterns are found in these two lineages of Stomiiformes. While the Gonostomata possess the usual distributed innervation pattern found in other teleosts, members within the Photichthya have the white zone of the myotome innervated in a different way. Terminal endplates are seen on many fibers which are probably innervated at

both ends. In addition, some axons pass from the myosepta into the midregions of the myotome to form a sparsely distributed innervation pattern. Thus, the Photichthya possess a third type of innervation pattern (Fig. 1C), distinct from either the terminal or distributed patterns, apparently combining elements of both.

7) Eurypterygii

All 125 species representing 99 genera examined in the Aulopiformes, Myctophiformes, Paracanthopterygii, and Acanthopterygii possess the distributed innervation pattern (see Table 1 for list of eurypterygians examined).

DISCUSSION

All non-teleost fishes possess terminally innervated white muscle fibers (Ono, unpublished). It is reasonable to suppose therefore that this pattern is the primitive condition and that the distributed pattern of innervation is derived. The universal occurrence of the distributed pattern in the Eurypterygii supports this view.

Two questions arise. First, is there a functional advantage in the distributed pattern that has led to its universal appearance in "higher" teleosts? Secondly, can white muscle innervation prove useful in dealing with the controversial questions of the limits and interrelationships of different teleost groups?

Consideration of the habits of fishes possessing the two types of innervation pattern, for example, *Hiodon* and *Heterotis* or *Albula* and *Chanos*, shows no obvious correlation between habitat and innervation pattern, nor any obvious differences in locomotor ability. But studies of fishes swimming under controlled conditions have revealed a notable difference in locomotor ability between fishes where the white muscle is innervated terminally, and where it is innervated in the distributed manner. Few fishes have yet been studied in this way (where activity in different zones of the myotome is monitored by electromyography as the fish swims at different speeds), but results are consistent, and are probably generally applicable. In all fishes studied, the red muscle fiber zone of the myotome is active during slow cruise swimming that can be maintained indefinitely. In fishes where the white muscle fibers are terminally innervated, these are only active during bursts of rapid swimming, and are rapidly exhausted (Bone, 1966; Bone *et al.*,

1978). Where the white muscle fibers are innervated in the distributed manner, they operate quite differently, for they are active not only during bursts of rapid swimming, but also during cruise swimming at intermediate speeds (Hudson, 1973; Johnston *et al.*, 1977; Bone *et al.*, 1978).

Electromyographic records from the white muscle zone during cruise swimming in such fishes are different from those obtained during rapid swimming, and it appears that where the fibers receive distributed innervation, they can operate in two ways propagating action potentials only during rapid swimming (Bone *et al.*, 1978). Extracellular recordings cannot provide other than suggestive evidence on this point, and definite proof of the hypothesis that contraction of the same fast muscle fiber in such fishes can either follow local potentials or propagated action potentials awaits intracellular investigation.

However, the results of these electromyographic studies clearly show that fishes with the distributed pattern of innervation of the white muscles are able to recruit these fibers to give a wider range of sustainable cruising speeds than can be obtained when the white fibers are terminally innervated and are used only during burst swimming. Evidently, this ability to swim for long periods over a wide speed range could confer a significant advantage to fishes in some particular habitats. For example, it may be advantageous to fishes living in streams where flow varies and the fishes are required to keep stationary. This ability to swim over a wide speed range would be insignificant to benthic fishes, however, at least in the adult stage due to the relatively stable flow regime of the water column.

We conclude that the distributed pattern of innervation was derived in teleostean evolution when adults or larvae were pelagic, and has been retained in those groups where the adults today are relatively sedentary, so that the habits of the adults today are not correlated with the innervation pattern.

The first attempt to use the innervation pattern as a systematic character made the simple assumption that this derivation from the ancestral terminal pattern occurred only once during teleost phylogeny (Bone, 1970). The present more complete survey (unfortunately still lacking data on several important species) demonstrates that this assumption can no longer by justified. Figure

2 shows a current view of the relationships among teleost groups (Fink and Weitzman, 1982), and indicates points where transition from terminal to distributed innervation is assumed to have taken place. In this view of the relationships of the groups, the change presumably took place independently on at least eight occasions.

In general, our survey has shown that the more primitive groups possess the terminal innervation pattern, as expected. Thus in the Osteoglossomorpha, the Hiodontoidei is a phylogenetic relict in the sense that the two living *Hiodon* species form a lineage that has retained a large number of primitive features (Greenwood, 1970); only these members of the group possess the terminal pattern.

Both the Elopomorpha and Clupeomorpha (with the sole exception of *Denticeps*) also possess the terminal pattern. The freshwater *Denticeps* retains many primitive characters, (Greenwood, 1968), but is unique among clupeomorphs in having achieved the distributed innervation pattern. Since a wider sustainable speed range might be a distinct advantage in the fluviatile freshwater environment, we examined other African freshwater clupeids, but all five genera studied possessed terminally innervated white muscle fibers.

In the Ostariophysi, all Gonorynchiformes and some Siluriformes have the terminal innervation pattern, and if the scheme of ostariophysan relationships proposed by Fink and Fink (1981) is accepted, this implies that convergent origin of the distributed pattern has occurred in all lines except that leading to the Gonorynchiformes (Fig. 2). Certainly, although the phylogenetic position of Siluriform families is uncertain, the innervation pattern is terminal in the most primitive, the relict Diplomystidae.

Perhaps the most interesting group with respect to muscle innervation pattern is the Stomiiformes. This group has been less thoroughly studied than the Ostariophysi, and despite recent work by Fink and Weitzman (1982), and an earlier study by Weitzman (1974), relationships within the group are still uncertain. It is notable that the two major sister groups forming the Stomiiformes, the Gonostomata and Photichthya (Weitzman, 1974), have different innervation patterns. In the Gonostomata, innervation is distributed, but in the Photichthya, innervation of the white fibers is mixed. Relatively few axons course through the white portion of the myotome, and in addition there are axons terminating on the fiber

ends as in the terminal pattern. Perhaps in this group of teleosts, we witness the distributed innervation pattern at an early stage in its development. It would be interesting to see whether the mixed pattern of adult photichthyans develops from an initially terminal pattern in the larval stage.

Few studies involving the nervous system in fishes have been used in a comparative fashion to solve problems of classification. On the whole, our survey suggests that the innervation of white myotomal fibers, despite evident convergence in its origin, should be considered a systematically useful character, and may prove particularly helpful in elucidating interrelationships within the Siluriformes and the Stomiiformes, respectively.

ACKNOWLEDGMENTS

We express our gratitude to Drs. P. H. Greenwood, William L. Fink, Karel F. Liem, Ian A. Johnston, as well as to Mr. Julian B. Badcock and Ms. Sara V. Fink for providing helpful comments and specimens. R. D. O. was partially supported with funds from a Raney Award (American Society of Ichthyologists and Herpetologists), National Science Foundation Grant BNS-7915308, and National Institutes of Health Predoctoral Fellowship GMO-7117 during the tenure of this project.

LITERATURE CITED

Barets, A. 1961. Contribution à l'etude des systèmes moteurs lent-et rapid du muscle latéral des téléostéens. Arch. Anat. Morphol. Exp., **50** (suppl.): 91–187.

Best, A. C. G., and Q. Bone. 1973. The terminal neuromuscular junctions of lower chordates. Z. Zellforsch., **143**: 495–504.

Bone, Q. 1964. Patterns of muscular innervation in the lower chordates. Int. Rev. Neurobiol., **6**: 99–147.

———. 1966. On the function of the two types of myotomal muscle fibre in elasmobranch fish. J. Mar. Biol. Ass. U.K., **46**: 321–349.

———. 1970. Muscular innervation and fish classification, pp. 369–377. *In* A. de Haro (ed.), I Simposio Internacional de Zoofilogenia, Fac. Ciencias, Univ. Salamanca, 492 pp.

Bone, Q., J. Kiceniuk, and D. R. Jones. 1978. On the role of different fibre types in fish myotomes at intermediate swimming speeds. Fish. Bull., **76**: 691–699.

Fink, S. V., and W. L. Fink. 1981. Interrelationships of the ostariophysan fishes (Teleostei). Zool. J. Linn. Soc., **72**(4): 297–353.

Fink, W. L., and S. H. Weitzman. 1982. Relationships of the Stomiiform fishes (Teleostei) with a description of Diplophos. Bull. Mus. Comp. Zool., **150:** 31–93.

Greenwood, P. H. 1968. The osteology and relationships of the Denticipitidae, a family of clupeomorph fishes. Bull. Br. Mus. Nat. Hist. (Zool.)., **16**: 213–273.

_____. 1970. On the genus, *Lycoptera*, and its relationships with the family Hiodontidae (Pisces, Osteoglossomorpha). Bull. Br. Mus. Nat. Hist. (Zool.)., **19**: 257–285.

Hudson, R. C. L. 1973. On the function of the white muscles in teleosts at intermediate swimming speeds. J. Exp., Biol., **58**: 509–522.

Johnston, I. A., W. Davidson, and G. Goldspink. 1977. Energy metabolism of carp swimming muscles. J. Comp. Physiol., **114**: 203–216.

Palmgren, A. 1948. A rapid method for selective silver staining of nerve fibres and nerve endings in mounted paraffin sections. Acta Zool., **29**: 378–392.

Rosen, D. E. 1973. Interrelationships of higher euteleostean fishes, pp. 397–513. *In* P. H. Greenwood, R. S. Miles, and C. Patterson (eds.), London, Academic Press, 536 pp.

Sakharov, D. A., and L. A. Kashapova. 1979. The primitive pattern of the vertebrate body muscle innervation: Ultrastructural evidence for two synaptic transmitters. Comp. Biochem. Physiol., **62**(A): 771–776.

Weitzman, S. H. 1974. Osteology and evolutionary relationships of the Sternoptychidae with a new classification of stomiatoid families. Bull. Am. Nat. Hist., **153**(3): 329–478.

Winkelmann, R. K., and R. W. Schmitt. 1957. A simple silver method for nerve axoplasm. Proc. Staff Meeting Mayo Clinic, **32**: 217–222.

Table 1. Patterns of Innervation in the White Myotomal Muscle Fibers of Teleosts.

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Osteoglossomorpha		
Notopteridae		
Notopterus chitala		+
Xenomystus nigri		+
Osteoglossidae		
Heterotis niloticus		+
Osteoglossum bicirrosum		+
Pantodontidae		
Pantodon bucholzi		+
Mormyridae		
Mormyrus sp.		+
Mormyrops engystoma		+
Gnathonemus petersii		+
Hiodontidae		
Hiodon tergisus	+	
Hiodon alosoides	+	
Elopomorpha		
Elopiformes		
Elopidae		
Elops sp.	+	
Albulidae		
Albula sp.	+	
Anguilliformes		
Anguillidae		
Anguilla sp.	+	
Muraenidae		
Gymnothorax sp.	+	
Congridae		
Conger sp. (2)	+	
Paraconger sp.	+	
Muraenesocidae		
Muraenesox sp.	+	
Ophichthidae		
Ophichthus sp.	+	

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers: Terminal Pattern	White Myotomal Muscle Fibers: Distributed Pattern
Eurypharyngidae		
Eurypharynx pelecanoides	+	
Notacanthiformes		
Halosauridae		
Halosaurus sp.	+	
Halosauropsis sp.	+	
Notacanthidae		
Polyacanthonotus sp.	+	
Clupeomorpha		
Clupeidae		
Clupea sp.	+	
Harengula sp. (2)	+	
Sardinella sp.	+	
Pellonula atzeliusi	+	
Opisthopterus sp.	+	
Limnothrissa miodon	+	
Thrissocles sp.	+	
Euplatygaster sp.	+	
Cynothrissa mento	+	
Poecilothrissa congicae	+	
Stolothrissa tanganicae	+	
Microthrissa sp.	+	
Opisthopterus sp.	+	
Alosa pseudoharengus	+	
Alosa aestivalis	+	
Alosa sp.	+	
Sprattus sprattus	+	
Engraulidae		
Anchoa mitchilli	+	
Anchoa sp.	+	
Chirocentidae		
Chirocentrus dorab	+?	
Denticipitidae		
Denticeps clupeoides		+
EUTELEOSTEI		
Ostariophysi		
Gonorynchiformes		

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Chanidae		
Chanos chanos	+	
Kneriidae		
Kneria mittei	+	
Phractolaemidae		
Phraetolaemus ansorgei	+	
Gonorynchidae		
Gonorynchus gonorynchus	+	
Characiformes		
Characidae		
Crenuchus spilurus		+
Hyphessobrycon flammeus		+
Hyphessobrycon serpae X *Hyphessobrycon collistus*		+
Hyphessobrycon pulchrspinnis		+
Astyanax mexicanus		+
Lebiasinidae		
Nannostomus nannostomus		+
Gasteropelecidae		
Gasteropelecus sp.		+
Hemiodontidae		
Hemiodus sp.		+
Cypriniformes		
Cyprinidae		
Notropis hudsonius		+
Cyprinus sp.		+
Gyrinocheilidae		
Gyrinocheilus aymonieri		+
Catostomidae		
Catostomus catostomus		+
Cobitidae		
Noemacheilus sp.		+
Siluriformes		
Siluroidei		

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Bagridae		
Parauchenoglanis macrostoma		+
Siluridae		
Kryptopterus bicirrhis		+
Malapteruridae		
Malapterurus electricus		+
Pangasiidae		
Pangasius sutchi		+
Chacidae		
Chaca chaca		+
Mochokidae		
Synodontis sp.		+
Aspredinidae		
Bunocephalus sp.		+
Callichthyidae		
Corydoras sp.		+
Hoplosternum sp.		+
Dianema sp.		+
Loricariidae		
Ancistrus sp.		+
Ictaluridae		
Ictalurus sp.		+
Diplomystidae		
Diplomystes sp.	+	
Ariidae		
Arius sp.	+	
Doradidae		
Doras sp.	+	
Pimelodidae		
Sorubim limas	+	
Pimelodella sp.	+	
Gymnotoidei		
Rhamphichthyidae		
Eigenmannia virescens		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Protacanthopterygii		
Salmoniformes		
Esocidae		
Esox niger		+
Esox americanus		+
Umbridae		
Umbra limi		+
Dallia pectoralis		+
Salmonidae		
Salmo trutta		+
Salmo sp.		+
Retropinnidae		
Retropinna sp.		+
Galaxiidae		
Galaxias sp.		+
Osmeridae		
Osmerus mordax		+
Plecoglossidae		
Plecoglossus altivelis		+
Argentinidae		
Argentina sp.		+
Opisthoproctidae		
Opisthoproctus sp.		+
Alepocephalidae		
Alepocephalus sp.	+	
Xenodermichthys copei	+	
Bathylaco nigricans	+	
Searsiidae		
Searsia sp.	+	
Stomiiformes		
Gonostomata		
Gonostomatidae		
Cyclothone obscura		+
Gonostoma elongatum		+
Maurolicus sp.		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers: Terminal Pattern	White Myotomal Muscle Fibers: Distributed Pattern
Sternoptychidae		
Argyropelecus sp. (2)		+
Sternoptyx sp.		+
Photichthya		
Chauliodontidae		
Chauliodus sp.	+	+
Stomiatidae		
Stomias sp.	+	+
Macrostomias longibarbatus	+	+
Astronesthidae		
Astronesthes sp.	+	+
Melanostomiatidae		
Melanostomias sp.		+
Eustomias sp.	+	+
Echiostoma barbatum	+	+
Malacosteidae		
Malacosteus sp.	+	+
Photostomias sp.	+	+
Idiacanthidae		
Idiacanthus sp.	+	+
EURYPTERYGII		
Aulopiformes		
Aulopodidae		
Aulopus sp.		+
Synodontidae		
Synodus sp. (2)		+
Giganturidae		
Gigantura sp.		+
Bathypteroidae		
Bathypterois sp. (2)		+
Myctophiformes		
Myctophidae		
Myctophum sp.		+
Diaphus sp.		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Paralepididae		
Paralepis sp.		+
Omosudidae		
Omosudis sp.		+
Evermannellidae		
Coccorella sp.		+
Scopelarchidae		
Scopelarchus sp.		+
Paracanthopterygii		
Gadiformes		
Moridae		
Antimora sp.		+
Macrouridae		
Nematonurus sp.		+
Lophiiformes		
Lophiidae		
Lophius sp.		+
Antennariidae		
Antennarius hispidus		+
Antennarius scaber		+
Acanthopterygii		
Atheriniformes		
Exocoetidae		
Parexocoetus sp.		+
Cypselurus sp.		+
Hemiramphus sp. (2)		+
Belonidae		
Belone sp.		+
Platybelone sp.		+
Tylosurus sp.		+
Cyprinodontidae		
Belonesox belizanus		+
Scomberesocidae		
Scomberesox sp.		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Atherinidae		
Menidia menidia		+
Atherinomorus sp.		+
Beryciformes		
Polymixiidae		
Polymixia lowei		+
Polymixia japonica		+
Holocentridae		
Holocentrus sp. (3)		+
Cetomimidae		
Cetomimus sp.		+
Melamphaeidae		
Melamphaes sp.		+
Dactylopteriformes		
Dactylopteridae		
Dactylopterus sp.		+
Zeiformes		
Zeidae		
Zeus faber		+
Sygnathiformes		
Aulostomidae		
Aulostomus sp.		+
Fistulariidae		
Fistularia sp. (2)		+
Sygnathidae		
Nerophis sp.		+
Hippocampus sp.		+
Scorpaeniformes		
Triglidae		
Trigla sp.		+
Cottidae		
Cottus cognathus		+
Perciformes		
Centrarchidae		
Pomoxis nigromaculatus		+
Lepomis gibbosus		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Priacanthidae		
Priacanthus sp.		+
Carangidae		
Caranx sp. (3)		+
Oligoplites sp.		+
Seriola sp.		+
Lutjanidae		
Lutjanus sp. (2)		+
Ocyurus sp.		+
Plectorynchidae		
Gaterin sp.		+
Pentapodidae		
Monotaxis sp.		+
Serranidae		
Epinephelus sp. (3)		+
Petrometapon sp.		+
Serranus sp.		+
Cephalopholis sp.		+
Pomadasyidae		
Haemulon sp. (2)		+
Anisotremus sp.		+
Percichthyidae		
Morone labrax		+
Sphyraenidae		
Sphyraena sp.		+
Grammistidae		
Rypticus sp.		+
Scaridae		
Sparisoma sp. (3)		+
Percidae		
Etheostoma olmstedi		+
Stromateidae		
Stromateid sp.		+
Istiophoridae		
Makaira sp.		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Coryphaenidae		
Coryphaena sp.		+
Sciaenidae		
Cynoscion regalis		+
Equetus sp.		+
Cichlidae		
Julidochromis sp.		+
Belontiidae		
Trichogaster trichopterus		+
Channidae		
Channa micropeltes		+
Mullidae		
Mullus surmuletus		+
Mulloidichthys sp.		+
Kyphosidae		
Kyphosus sp.		+
Chaetodontidae		
Chaetodon sp. (6)		+
Pomacanthus sp.		+
Pomacanthodes sp.		+
Pomacentridae		
Abudefduf sp.		+
Cepolidae		
Cepola rubescens		+
Centropomidae		
Centropomus sp.		+
Acanthuridae		
Adanthurus sp. (4)		+
Zanclus sp.		+
Scombridae		
Scomber sp. (2)		+
Thunnus sp.		+
Euthynnus sp.		+
Gerreidae		
Gerres sp.		+
Eugerres sp.		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Siganidae		
Siganus sp.		+
Labridae		
Halichoeres sp.		+
Lepidaplois sp.		+
Anampses sp.		+
Lachnolaimus maximus		+
Gobiidae		
Periophthalmus koelreuteri		+
Ephippidae		
Chaetodipterus sp.		+
Tetraodontiformes		
Balistidae		
Balistes sp.		+
Xanthichthys sp.		+
Melichthys sp.		+
Cantherhines sp.		+
Balistapus sp.		+
Ostraciotidae		
Acanthostracion sp. (2)		+
Lactophrys sp.		+
Diodontidae		
Diodon sp. (2)		+
Chilomycterus sp.		+
Tetradontidae		
Sphoeroides sp.		+

In all the fishes listed above, the red myotomal muscle fibers had the distributed pattern of innervation.

MUS. COMP. ZOOL
LIBRARY
MAR 1 8 1985
HARVARD
UNIVERSITY

B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 30 JUNE 1982 NUMBER 471

ARTHUR LOVERIDGE—A LIFE IN RETROSPECT

ERNEST E. WILLIAMS[1]

On February 16, 1980, at the age of almost eighty-nine, Arthur Loveridge, former Curator of Reptiles and Amphibians at the Museum of Comparative Zoology, died on the island of St. Helena in the South Atlantic after a short illness.

In 1924 A. Lawrence Lowell, then President of Harvard, wrote to the Immigration Department in Boston in these terms:

"This is to inform you that Arthur Loveridge, Esq., formerly of the Manchester University Museum, National Museum of Wales, and latterly Director of the British East African Museum in Nairobi, a gentleman standing high in his chosen field, is due on the steamer Laconia, arriving in Boston on or about May 1st.

"On March 14th of this year Mr. Loveridge was appointed by the Faculty of the Museum of Comparative Zoology in Harvard University to the position of Associate in Zoology in the Harvard University Museum, where he will exercise his profession during the coming years as an officer of Harvard University.

"Since I am informed that the British quota is full, I am anxious that you should know in advance that Mr. Loveridge is a teacher, scientist and author of high professional standing, and that he comes here already appointed to a University position in Harvard.

"Any kindness you may show him in expediting his entry will be very greatly appreciated by me."

It is obvious that President Lowell's plea was effective. It is known that Glover Allen, then Curator of Mammals, met Loveridge

[1]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

at the boat and drove him to Cambridge, where he was to spend thirty-three years (till 1957). At first he was Thomas Barbour's assistant, reorganizing the Museum's herpetological collection and then, when Barbour was appointed Director of the Museum, continuing to supervise with surpassing care the expansion of one of the world's great collections of reptiles and amphibians. From 1931 he had the volunteer assistance of Benjamin Shreve.

Thomas Barbour brought Loveridge to the New World, but Loveridge's heart remained in the continent of Africa where he had spent almost ten years. There he had made the reputation that brought the Harvard appointment. There he had met his wife, and there he had indulged to the full his passion for collecting and for general natural history that had been his since childhood—indulged it despite (or by means of) service with the East African Mounted Rifles, the Nairobi Museum, and the Game Department in Tanganyika (now Tanzania).

Loveridge's association with Harvard was no bolt from the blue; it was a tie that had gradually strengthened. In the Museum Report for 1919–1920, there is a mention of a first gift from Loveridge. His name recurs in 1921–1922, and then, in 1923–1924, there is Barbour's comment: "This year has been eventful in that during its course the Arthur Loveridge African collection was received and Mr. Loveridge arrived to assist in a general overhauling of the study series."

Harvard got a bargain in Loveridge. Harvard bought Loveridge's collection, but with it came a Curator—one the collection desperately needed. The other side of Loveridge's passion for collecting was a passion for order and for tidiness: what he brought back or had brought back to him had to be as perfectly classified, ticketed, and put away as human power could manage.

For a while he surely had the best of his two worlds. On the one hand, he was in charge of a major but crowded, ill-labeled, ill-organized gathering of collections. He was able to transform it into a model of collections as he felt they should be—taking frogs, snakes, and lizards out of tanks and putting them in fine glass-stoppered bottles with labels written in hard pencil in his own neat hand and carefully arranging them within trays, each with neatly typed labels. *His* collection, when he finished, was a thing of beauty (and fiercely kept so).

For the other part, in the first years he was repeatedly able to go back to Africa and, doing what he most wanted to do, simultaneously enrich the Harvard collections and provide for himself the study material he needed. Clearly this had been part of the understanding that went with the Harvard appointment. He did general collecting, not only herpetological collecting. He had always done so, and museum workers in that day were always, whatever their specialty, general collectors. He did sometimes collect large mammals, but this, I am told, was not to his preference. He did get to Africa and to parts of it he had not seen before. In the years between 1924 and 1940 he was away from Cambridge four times (1925–1926, 1928–1929, 1933–1934, and 1938–1939). On each occasion he was away a full year. In terms of his additions to the Harvard collections, this was his prime time.

The first years were active years in many ways. These were years of affluence for the Museum. Barbour's money immensely augmented collections that Louis Agassiz had been at feverish pains to acquire. Although Loveridge's African expeditions were undoubtedly the greatest source of additions to the herpetological collections during these years, Barbour did not cease, so long as he was able, to encourage and directly finance every sort of acquisition from any part of the world. This flood of material was certainly Loveridge's joy.

Loveridge was something of a public figure in the first years. He routinely gave lectures, wrote articles for "Fauna," "Frontiers," and "Natural History" and in 1928 gave a series of twenty lectures for the Boston Society of Natural History on Boston's WBET entitled "Tales from Tanganyika." He made "Who's Who" in 1938.

There is much to indicate that the world changed for Loveridge after the 30s. The Depression had come; if its impact was not immediate, it was fundamental. The concomitant diminution of Barbour's fortune meant that the flood of specimens began to come to an end. (Loveridge once showed me how plainly this change was demonstrated on our species cards.) It was later in this period of diminished affluence that Loveridge refused to take more than two of a series, offered by Vanzolini, of a species not represented in the MCZ collections; "Bottles," he is reported to have said, "are precious." For some time the momentum of previous activity continued. By 1942, the number of species and subspecies in the

collection surpassed 6,000. The Department had to be enlarged, and a new room (the old Aquarium) was taken over for snakes.

But already in the previous year (1941), Barbour's report as Director had begun to take a mournful tone: "Increased taxes are going to make it difficult or impossible for the Museum to expect to receive the private assistance which it has received in the past."

In 1942 Shreve left for the army. In 1942–1943 only 400 specimens were catalogued; 140 of these were exchanges. Loveridge's own collecting suffered also. There was to be only one more African trip.

Decreased curating and collecting did not impair Loveridge's productivity, however. His previous work had been primarily reports of collections and faunal studies. He now began revisions, and in a popular vein began the series of books that gave him wider fame. "Many Happy Days I've Squandered" (1944) was the first. "Tomorrow's a Holiday" succeeded it in 1947, then "I Drank the Zambesi" (1953), and "Forest Safari" (1956). All included accounts, highly entertaining, of his African experiences.

The end of the Second World War had brought some bonuses. Shreve came back. W. H. Stickel, Sergeant Beck, Captain Jarvo, an Australian, Gunner Tovell, and others sent to Loveridge material from the Pacific area collected during their service. Loveridge had written a little book, "Reptiles of the Pacific World" (100,000 copies were printed for the Armed Forces, and it has recently been reprinted), and these collections were its rewards. Loveridge dutifully reported on the collections and on similar material obtained by the National Museum.

(It is curious that the most massive of all the acquisitions since Loveridge were the result of these activities peripheral to Loveridge's major interest. Correspondence with Fred Parker in 1960 was initiated by a request for Loveridge's Australian and New Guinean papers and has resulted in the MCZ's now huge Solomons and New Guinea collections.)

Loveridge remained in charge of the collections for almost ten years more. He made the last African expedition of his Harvard career, that to Nyassaland and Tete in 1948–1949. Thereafter, the entire period was devoted to his intended summary of East African herpetology, most of it to the series of revisions that he had begun earlier, in 1940, with some snake genera, and that culminated with the East African Check List published in the year of his retirement, 1957. One paper on "The Cryptodira of Africa" was in collaboration

with the man who was to succeed him—myself—published again in 1957.

Loveridge left Cambridge in 1957, immediately after his retirement, for the island of St. Helena in the South Atlantic. Although he did visit England, and I once saw him in the British Museum, and although we maintained a correspondence and he even published on material he sent to the Museum, he never returned to the United States. It is not known why—perhaps because the collection was no longer *his* in the special sense that it had been for thirty-three years.

The *Boston Globe* of July 21, 1957 headed its four column account of Loveridge's retirement with the statement: "Retiring Curator to Avoid Work Temptation." If that was genuinely Loveridge's intention, it did not turn out that way. He did make his retirement home at Varney's on St. Helena, but it often seemed that he was only a little less active in these final years than he had been in the MCZ.

He kept up an intense interest in both African herpetology and the Museum and in collecting: his letters of 1958 are full of impatience to get the tubes to collect St. Helena spiders. His correspondence, in fact, began on the boat to the island, and he was soon to start numbering his letters. There were already 2,472 in early 1965, and they were nearing 7,000 at the time of his death. (He was a punctilious writer, always answering a letter, but always insisting also that his letters be answered before he would write again.)

He travelled also, not infrequently to England, and at least once collected again in Africa—a small collection—*Chamaeleo, Mabuya,* and frogs from Mau Narok at 9,000 ft. in Kenya, donated to the MCZ. He received specimens from correspondents also and published on some of them, reporting *Hemidactylus mercatorius* as new to Ascension Island and describing new amphisbaenids collected by Ionides in Tanganyika. His most interesting paper from his "exile" on St. Helena may be unique in herpetology: his own report, published at his own expense, on "The status of new vertebrates described or collected by Loveridge."

His wife died suddenly on St. Helena in 1972. His son Brian joined him on the island four years later. In another four years Loveridge himself was dead.

What of the man behind the Curator? He was, of course, a very special individual in his own right, but he was also one of a breed that is now extinct because the times have made its life style no longer viable.

Born in Penarth, Glamorgan, Wales, 28 May 1891, Loveridge was thirty-three when he came to the Harvard Museum. He had already been Curator in Nairobi and served in museums in Wales and England. As he reports in "Many Happy Days I've Squandered," he had decided to become a Museum Curator at the age of ten. He tells in the preface of that book of "the acquiescence of a kindly father." However, the Harvard Archives contains his application in 1914 for the newly created post of Curator at the Nairobi Museum. This reveals that he had to "serve time" for two years as apprentice in the family business of ship furnishing, and that only then was he allowed to take a year's course in Zoology and Botany in the University College of South Wales on the way to appointments first at the Manchester University Museum and then in the Temporary Museum in Cardiff.

It was while he was in the latter post, and, in addition to his regular duties, making a card index of the whole British Fauna (about, he reports, 23,000 cards), that he serendipitously received knowledge of an open position in Africa. Although he already had a private collection of "nearly 250 jars of preserved reptiles and over 300 glass topped drawers containing birds' eggs, insects and other specimens," he was always avid for more. When he heard about a civil engineer from British East Africa due home on leave who "had in his youth shown a fondness for snakes," he tried to inveigle the man into collecting for him. Utilizing a joint interest in stamps and bribing him with duplicates of these, Loveridge extorted a promise to pickle lizards and snakes. An inquiry six months later produced an apologetic reply which included the news that the East Africa and Uganda Natural History Society needed a curator for a new museum that would have government support. "Why don't you apply for the post and then you can collect your own bally snakes" was the advice. Loveridge applied at once, was accepted, and arrived in Nairobi in mid-1914.

The first World War very soon cast its shadow over Africa; it did not interrupt Loveridge's career as a naturalist. Although he joined the local forces shortly after his arrival and after six months' training was on active duty, it is often difficult, from his account of the next four years, to be conscious that a war was on. The occasional moment of danger was memorable for him because of the capture of a rare animal. His story of the capture of his first *Boulengerula boulengeri* is characteristic: "This rare Caecilian was

obtained under rather unusual circumstances during the East African campaign. We were busily engaged in 'digging in' under an unpleasant shellfire, when it was unearthed by one of my fellow troopers in the Mounted Rifles. He humourously called out that one of my snakes had escaped and that, if I did not come over and take charge of it at once, he would run his bayonet through it. Needless to say, when I saw what it was, I very gladly took charge of it." The same total devotion to natural history made him—as he himself recounts—badger first his sergeant and then the general in the midst of his staff for permission to obtain bottles of pickled snakes from an abandoned German house.

He got the snakes; this was no isolated incident. One of his periodical summaries of his activities preserved in the Harvard Archives mentions: "Travelling through German East Africa from north to south provided exceptional opportunities for collecting . . . All necessary preservatives and pickling jars were 'found' in captured German towns." (The 'found' is in quotation marks in his own typescript.)

We have here the image of a man wholly devoted to an avocation that he made his vocation and who found his life "one long holiday. Gratefully I confess to being one of the favored few whose waking thoughts in the morning consist of the pleasant planning of the day's work." It was he who also wrote: "Probably only a zoologist can look at an uncaught cobra and feel the joy a child feels on Christmas morning."

It is this spirit of Loveridge that is well-caught in the cartoon that I have chosen to illustrate this memorial of a life. It is a man I would have liked to have known. It is not, I think, the man I knew.

I came into Loveridge's ambience late, in 1947, after the Second World War, and while I was working on my thesis. Visiting the Museum, I was able to re-identify one or two turtles and so gained his confidence. This began a cordial relationship. Eventually, after I came to Harvard, I was able to call him "Arthur." (The first level of intimacy was "Loveridge" rather than "Mr. Loveridge.")

The man I knew was stiffish. Some called him "Sir Arthur." This was probaby mere Englishness plus a firm insistence on standards that he did not allow to be relaxed, not for himself, not for anyone. Romer called him the "Demon Curator," and this was the aspect that most of us knew, who knew him late in his career.

He could be kind and very helpful. Many of his correspondents,

the visitors to the Department, the young questioner, and even some of the anatomists in search of specimens for study knew his kindness and assistance well. The more demanding might get short shrift, and for poseurs and frauds—so he regarded Ivan Sanderson—he had no kindness at all. His review of a book of Sanderson's, and of its gentler reviewers, is classic vitriol.

His tidiness extended to classification. He preferred clarity, was unhappy with complication, was impatient of subtlety. He wanted problems solved cleanly, once and for all. Therefore he was very much a lumper. He was so much a lumper that many of our species cards record the species name with an interval between the genus and species name—an interval for the eventual insertion of the species name of which Loveridge was sure the taxon in question could only be a subspecies. (He was very insistent also that subspecies be readily recognizable from museum material. He reportedly gave K. P. Schmidt the chance to sort out unlabelled MCZ specimens into subspecies that K. P. was describing: K. P. flunked. It is known that he gave a similar test to Vanzolini on the subspecies of *Amphisbaena fuliginosa* that Vanzolini passed handsomely. Vanzolini is now not certain that one of his subspecies is valid.)

This fervor for lumping and tidiness sometimes caused disagreements. I was invited into collaboration with him on the Cryptodira of Africa. As he told me, this was partly because I knew turtles, but also because I could read German and translate type descriptions. That the collaboration succeeded is evidenced by a thickish volume, but there were moments of discord. My discussions were too theoretical and too verbose, and my taxonomy too splitting. Loveridge told me that he had lost a year of his scheduled program because of me, and a well-known footnote (softened at the advice of his wife) testifies to our taxonomic disagreement. (It was characteristic of him that this did not impair a good relationship.)

I, and others of my time, knew Loveridge only in the Curator-facet of his life. We knew him after his last field trip. That part of his life had ended.

But more, I think, was gone by then than just the opportunity for year-long field trips. The world had changed. The British Empire was diminished if not extinct. Africa had changed, Harvard had changed. His chosen profession as naturalist-curator was no longer highly regarded at Harvard, or elsewhere. Africa was not the same

Cartoon of Arthur Loveridge from the newspaper *East Africa*.

land in which Salimu, his favorite No. 1 Boy, had chosen to be naturalist-servant to a naturalist-master.

It is notable that he did not choose to go back to Africa upon his retirement. There is a story that his wife chose isolated St. Helena because they had once stopped there on their way to Africa in one of the two months of the year when the climate is pleasant. But surely, even if that were true, the choice involved more than that. Africa was no longer the Africa he had loved.

The man of the later years was not, at least on the surface, the man one would expect to write a book with the title "Many Happy Days I've Squandered." The man seemed sterner and more prim, more *New England*—as though he had acquired the characteristics of the New England breed for whom the verb "to squander" borders on obscenity.

Loveridge's aspect as Demon Curator provoked as much astonishment as appreciation. Romer, the new Director after Barbour, regarded Loveridge with a respect not unmixed with amusement. Their psychologies were nearly antithetical, and Romer's appreciation of Loveridge's value was very incomplete. It is true that Loveridge could not have been quite happy with Barbour's exuberant and insouciant carelessness, but at least Barbour and Loveridge were of one mind about collecting and collections. Romer marked the first of the transitions to another museum style.

The element of fanaticism in Loveridge's neatness quite naturally evoked legends. There is a tale that there was in the Department a drawer labelled "string too short to use." Neatness and routine were at times extreme. Shreve's work counter had to be cleared at 4:30 when he left. Books had to be put back. Loveridge told both Carl Gans and Vanzolini that gaps on the book shelves were to him like teeth that had been knocked out. Even the chairs had to be in correct positions under the counter. I was reprimanded one Monday, when, working over a weekend, I left all three chairs improperly aligned.

Loveridge's fanatic passion for his collection astonished his colleagues; clearly he did not fit too well in the new world at Harvard. But fanatic attention to detail is a good thing in a curator, and certainly the Museum was well served by Loveridge's devotion. The organization of the herpetology collection was his and his alone; the task that confronted him when he first arrived must have been fabulous, and the order he achieved remains an achievement as

great as his African contributions. When I took over the collection, all was in perfect shape. There were few curatorial tasks to do: only the one collection from the Riu-Kiu Islands that had not yet been wholly identified and put away.

Loveridge served in a University Museum, but he was in no sense an academic. He belonged to another generation and another life style—he was pre-eminently a collector-naturalist. It is interesting to put him in context in the succession of herpetological curators at the MCZ. Agassiz must be counted here, but he was clearly unique—a European emigre, professor, builder and acquirer of collections, intellectual parent to whole generations of natural historians in the United States, he is not at all comparable to anyone else.

Of Garman, the next in line, we know too little, not much beyond Barbour's unsympathetic remarks and some plaintive autobiographical notes of his own. Before the MCZ, he apparently had an irregular career; at the MCZ, *fide* Barbour, he remained isolated and apart. Clearly in his day he was useful and respected. He began the MCZ's West Indian interest which Barbour so much cultivated after him.

Barbour had, in contrast, the full academic panoply, a doctoral degree, and, at least late in life, professorial status. For all that, he was throughout his life the Wealthy Amateur, never quite willing to go very deep, never quite serious enough to be professional. He could be pontifical and very disparaging of others, but many of the criticisms could have been turned against him. He had notable protegés—G. K. Noble and E. R. Dunn—and was, within American herpetology, for a while something of a father figure with equal colleagues but no admitted superior.

Loveridge was very different. British always and a Briton of the Empire, he was a man who, without inherited wealth, had chosen, very stubbornly, a poorly remunerative career—the career of Bates and Wallace, the naturalist-collector. He had chosen also a continent. His eyes and his interests turned eastward toward Africa; he was hardly part of American herpetology. For all that in Cambridge he was physically close to his American colleagues, it was hardly different from what it might have been had he been across the sea. If ever he was further west than New York, I have no record or report of it.

In a sense that Barbour was not, Loveridge was a professional. Without interest in theory or in biology beyond field and museum

natural history, he was totally professional in what he did—completely dedicated to competence in that rather narrow area. He never formally taught, and his own formal instruction was limited. In herpetology, like his predecessors (and like myself), he was self-taught. (The new curator at MCZ is the first to have had formal specific instruction in herpetology.) What he chose to be, he was *par excellence*—Curator-Collector-Naturalist.

With Loveridge's departure—and his literal departure from Cambridge for St. Helena came only a few weeks after his formal retirement as Curator—the Department settled into quite another style. I was the first curator to be fully a product of Academia—not only the holder of the conventional degrees, but one who needed them for a living. The world has changed post-Loveridge; the pure naturalist-collector is, when he exists at all, an anachronism.

Arthur and Mary Loveridge's one son, Brian, was schooled at Harvard, and had early gone to England for his career. Apart most of their lives, Brian joined his father on St. Helena and was building a home there near Varney's when his father died. Brian has said of his father that his work was his life. That is an affirmation that is also a tribute, and the tribute that Arthur Loveridge would have most wanted.

In one of the entryways to the MCZ there is a plaque on the wall honoring Alexander Agassiz and with the Latin motto, "Omnia quae hic vides monumentum." The Herpetology Department might very reasonably display a similar motto in Loveridge's honor. The collection's order and style have his imprint. I have added somewhat to that collection, but he provided the solid base.

His taxonomic work is now history; his revisions are now revised. It would disappoint him bitterly that this is true, but his passion for simplicity is now judged to have gone too far. He was concerned in his "Status" paper to learn—certainly with a twinge of heart—which of his species had been synonymized. He would view with dismay, if not distaste, the sibling species that are now commonplace. He would not understand the concerns and disputes of modern taxonomists, nor care to. In this sense time has passed him by, but his own collections and the collections he so diligently curated are his enduring monument.

MUS. COMP. ZOOL
LIBRARY
MAR 18 1985
HARVARD
UNIVERSITY

BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 30 JUNE 1982 NUMBER 472

FISHES OF THE SUBORDER LABROIDEI (PISCES: PERCIFORMES): PHYLOGENY, ECOLOGY, AND EVOLUTIONARY SIGNIFICANCE

LESLIE S. KAUFMAN[1] AND KAREL F. LIEM[2]

ABSTRACT. We postulate that the Pomacentridae, Cichlidae, Embiotocidae, Labridae, Odacidae, and Scaridae comprise a monophyletic assemblage: the Labroidei. Four groups within the Labroidei can be defined as monophyletic assemblages on the basis of shared derived characters: the Pomacentridae, Cichlidae, Embiotocidae, and Labridae (which includes the Scaridae and Odacidae). The Pomacentridae is considered the primitive sister group of all other Labroidei; the Cichlidae is a sister group of embiotocids and labrids, and the Embiotocidae is a sister group of the Labridae. Labroids are characterized by (1) united or fused fifth ceratobranchials resulting in the formation of one functional unit; (2) a true diarthrosis between upper pharyngeal jaws and the basicranium without an intervening part of the transversus dorsalis anterior muscle; and (3) the presence of an undivided sphincter oesophagi muscle forming a continuous sheet. It is proposed that (1) the ecological and functional versatility of the trophic apparatus is correlated with a characteristic structural design, and that (2) this design has contributed to the dominant position of labroids in diurnal communities of tropical marine and lentic fresh waters.

INTRODUCTION

Liem and Greenwood (1981) have recently reviewed the comparative functional morphology of the pharyngeal jaw mechanism in acanthopterygian fishes. On the basis of functional considerations they have proposed that the Cichlidae, Embiotocidae, Labridae, Odacidae, and Scaridae comprise a monophyletic assemblage.

[1,2] Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

Pharyngognathy, as expressed in the Cichlidae, has been correlated with several functional and ecological attributes which distinguish cichlids from most other Acanthopterygii. First, cichlids can mechanically process a broader range of food types (Liem, 1974). Second, they have greater feeding versatility (Liem and Osse, 1975; Liem, 1980) and hence a broadened fundamental niche (*sensu* Hutchinson, 1958, 1965). Finally, cichlids exhibit an extremely high species diversity, perhaps because extinction rates in changing environments are decreased (Liem, 1982). To test this hypothesis, evolutionary patterns in the Cichlidae must be compared with those of related fishes both more and less specialized with respect to pharyngeal jaw morphology. Such an analysis requires a thorough knowledge of phylogenetic relationships (Lauder, in preparation). In this paper we offer a revised hypothesis of the phylogenetic relationships of pharyngognath acanthopterygians first proposed by Liem and Greenwood (1981). New morphological evidence offered here and by Stiassny (1981, personal communication) requires the inclusion of the Pomacentridae in the monophyletic assemblage Pharyngognathi (*sensu* Liem and Greenwood, 1981), and a rearrangement of the Embiotocidae as the sister group of the Labridae instead of the Cichlidae. The resulting scheme of classification is as follows:

Suborder Labroidei
- Family Pomacentridae
- Family Cichlidae
- Family Embiotocidae
- Family Labridae (including Labridae, Odacidae, Scaridae)

The proposed phylogenetic relationships provide a basis for assessing patterns of change in the feeding apparatus, historical consequences of new feeding mechanisms, and the evolution of coral reef fish communities.

MATERIALS AND METHODS

Morphological studies were conducted with the aid of a Wild-M5 dissecting microscope and camera lucida. Clearing and staining followed the techniques of Taylor (1967). Scanning electron microscopy was conducted on an AMR-1000, and x-ray cineradiography of feeding labrids and cichlids was carried out using the Siemens Cineradiographic Unit at 150 frames sec^{-1}. The following material was examined:

Pomacentridae: *Abudefduf taurus* MCZ 42755, *Amphiprion xanthurus* MCZ 14852, *A. percula* MCZ 33399, *Dascyllus trimaculata* MCZ 14837, *D. albisella* MCZ 51671, *Eupomacentrus planifrons* MCZ 44745, *E. acapulcensus* MCZ 43961, *Pomacentrus* littoralis MCZ 5794, *Chromis atrilobatus* MCZ 44640.

Cichlidae: *"Haplochromis" leuciscus* MCZ 49517.

Embiotocidae: *Rhacochilus vacca* MCZ 57708, *Damalichthys vacca* MCZ 54333, *Cymatogaster aggregata* MCZ 57707, *Phanerodon furcatus* MCZ 54334, *Embiotoca jacksoni* MCZ 54332.

Labridae: *Tautogolabrus adspersus* uncat., *Tautoga onitis* uncat.; *Halichoeres bivittatum, Scarus croicensis, Sparisoma viride,* all MCZ acq. 1981-002-6.

Caribbean reef fishes were studied in Salt River Canyon and Tague Bay, St. Croix, U.S. Virgin Islands, and also studied at the Discovery Bay Marine Laboratory, Jamaica, W.I. Ecological classifications of reef fishes were based in part on observations made from the NULS-1 Hydrolab during mission 81-8.

ANALYSIS OF CHARACTERS

Definition of the Labroidei

We postulate that the Pomacentridae, Cichlidae, Embiotocidae, Labridae, Odacidae, and Scaridae comprise a monophyletic lineage, the Labroidei. A cladogram defining this group and expressing relationships among its major clades has been derived on the basis of three investigations: Liem and Greenwood (1981), Stiassny's analysis of the phylogenetic relationships of the Cichlidae (in which extensive out-group comparisons are described, Stiassny, 1981 and personal communication), and this study (Fig. 1).

All Labroidei share the following three derived characters: (1) junction or fusion of the two fifth ceratobranchial bones into a single unit, (2) diarthrosis between the upper pharyngeal jaws and the basicranium (Fig. 2 A–F: APU; Stiassny, personal communication), and (3) the presence of the sphincter oesophagi muscle as a continuous sheet, with no dorsal subdivision (Fig. 2; Stiassny personal communication). Within Perciformes, fused or joined lower pharyngeal jaws also occur among the Anabantidae (all), Kyphosidae (*Girella tricuspidata*), and Sciaenidae (*Pogonias chromis* and *Aplodinotus grunniens*). The pharyngeal jaw morphology and biting mechanisms of these fishes differ appreciably, however, from those of the Labroidei (Liem and Greenwood, 1981). Other acanthopterygians show some form of articulation between the upper pharyngeal jaws and the basicranium (e.g., Sparidae,

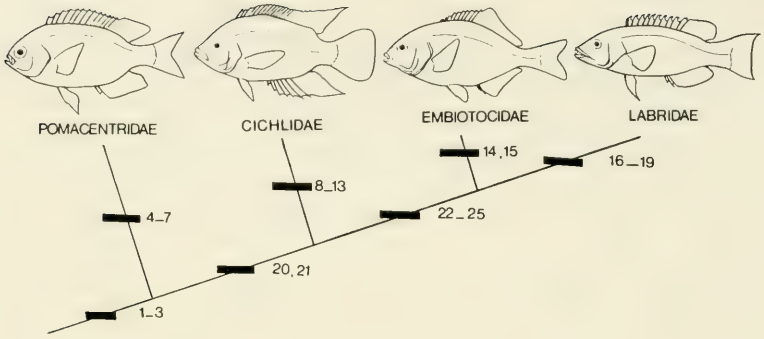


Figure 1. Cladogram illustrating interrelationships of the major labroid clades. Bars represent shared derived characters: (1) United or fused fifth ceratobranchials; (2) True diarthrosis between upper pharyngeal jaws and basicranium; (3) Undivided sphincter oesophagi muscle; (4) Strong sheet of connective tissue joining lower jaw with a ligament which inserts on the ceratohyal bone; (5) Nipple-like bony process on ventral surface of lower pharyngeal jaw; (6) Pharyngo-cleithral articulation of characteristic form; (7) Obliquus posterior dominant muscle to lower pharyngeal jaw; levator externus 4 and obliquus posterior vertically aligned on fourth epibranchial, separated by oblique aponeurosis or tendon; (8) Transverus dorsalis muscle subdivided into four parts; (9) Premaxillae and maxillae functionally decoupled; (10) Cartilagenous cap on anterior border of epibranchial 2; (11) Microbranchiospinae of characteristic form present on outer faces of second, third, and fourth gill arches; (12) A_2 and A_w portions of adductor mandibulae complex lacking major structural association; insertion of large ventral division of A_2 onto angulo-articular; (13) Head of epibranchial 4 distinctly expanded; (14) Intra-uterine development of young with strongly modified vascularized median fins; (15) Muscular sheet joining A_1 and $A_{2,3}$ portions of adductor mandibulae; (16) Levator posterior dominant muscle to the lower pharyngeal jaw, forming a force couple with the pharyngocleithralis muscle; (17) Toothplates of fourth pharyngobranchials absent (either lost or fused with pharyngobranchial 3), first pharyngobranchials absent or reduced; (18) Fourth epibranchials highly modified, articulating with upper pharyngeal jaws; (19) True pharyngo-cleithral articulation functioning as sliding and hinge joint; (20) Levator externus 4 is a continuous muscle joining prootic region to muscular process on lower jaw; (21) Predisposition for insertion of levator posterior muscle on lower pharyngeal jaw; (22) Loss of second pharyngobranchial toothplates; (23) First three branchial adductor muscles cover anterodorsal faces of the epibranchials; (24) Ligament connecting postmaxillary process of maxilla with anterior border of palatine and ectopterygoid; (25) Tooth rows arranged radially across the lower pharyngeal jaw, teeth located directly over the symphysis between left and right fifth ceratobranchials. LPJ toothplate composed of an anterior, small-toothed field and a posterior, large-toothed pavement replaced by addition along the rear margin of the LPJ.

Gerreidae, *Pogonias, Aplodinotus*), but only in the Labroidei is there a true diarthrosis. In other perciforms a portion of the transversus dorsalis muscle or its aponeurosis passes between the apophyses of the upper pharyngeal jaws and basicranium (Stiassny, 1981).

Synapomorphies Characterizing the Pomacentridae

The damselfishes can be defined on the basis of four characters. (1) Stiassny (1981: 286) observed that "A strong sheet of connective tissue originates from the dorsal border of the bony ridge on the medial face of the lower jaw [dentary] and merges with a cylindrical ligament that passes posteriorly and inserts onto the ceratohyal bone." In other acanthopterygians she examined this ligament was wanting. The remaining three characters concern the structure of the lower pharyngeal jaw (LPJ). (2) The LPJ's of all pomacentrids we have examined bear on their ventral surfaces a pair of small nipplelike processes, which serve as the insertion sites for the pharyngohyoideus muscle. These processes are absent in all other acanthopterygians examined. (3) In primitive acanthopterygians there is no contact between the fifth ceratobranchial and the cleithrum. In most pomacentrids, however, the muscular processes of the LPJ abut upon the cleithrum and slide along it by means of articular facets. Two such facets may be present (e.g., *Pomacentrus littoralis,* MCZ 5794): a dorsal facet lying parellel to the dorsoventral plane, and a ventral facet which is curved slightly outwards from this plane and may provide the LPJ with some lateral freedom of movement. Labrids, in contrast, have a true pharyngo-cleithral joint. The degree of pharyngo-cleithral articulation varies considerably among pomacentrids. Even when the two bones are closely related, the nature of the articulation differs from that seen in the Labridae (Liem and Greenwood, 1981). This difference is also reflected in the unique and complex shape of the muscular processes of the LPJ in pomacentrids, a feature related to their peculiar musculature (Figs. 2, 3). In some pomacentrids (e.g., *Microspathodon*) pharyngo-cleithral articulation appears to have been lost as part of a general reduction of the pharyngeal apparatus. (4) In pomacentrids, as in all more primitive perciforms, the fourth levator externus muscle (Fig. 2 A–F: LE_4) and levator posterior (LP) insert

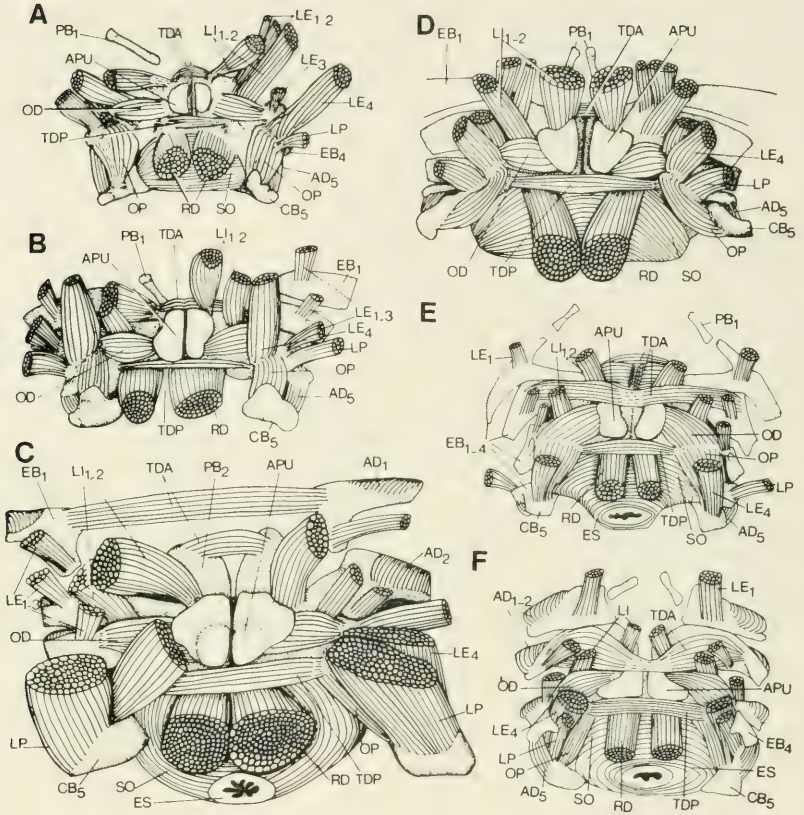


Figure 2. Dorsal aspect of the branchial musculature viewed from posterior to elucidate the muscles surrounding the esophagus and posterior branchial arches. A) *Pomacentrus littoralis;* B) *Abudefduf taurus;* C) *Tautogolabrus adspersus;* D) *Amphiprion xanthurus;* E) *"Haplochromis" leuciscus;* F) *Embiotoca jacksoni.*

Abbreviations: AD, adductor branchialis; APU, apophysis of upper pharyngeal jaw (third pharyngobranchial); CB_5, fifth ceratobranchial (lower pharyngeal jaw, LPJ); EB, epibranchial; ES, esophagus; LE, levator externus muscle; LI, levator internus muscle; LP, levator posterior muscle; OD, obliquus dorsalis muscle; OP, obliquus posterior muscle; PB, pharyngobranchial; RD, retractor dorsalis muscle; SE, sphincter oesophagi muscle; TDS, transversus dorsalis anterior muscle; TDP, transversus dorsalis posterior muscle.

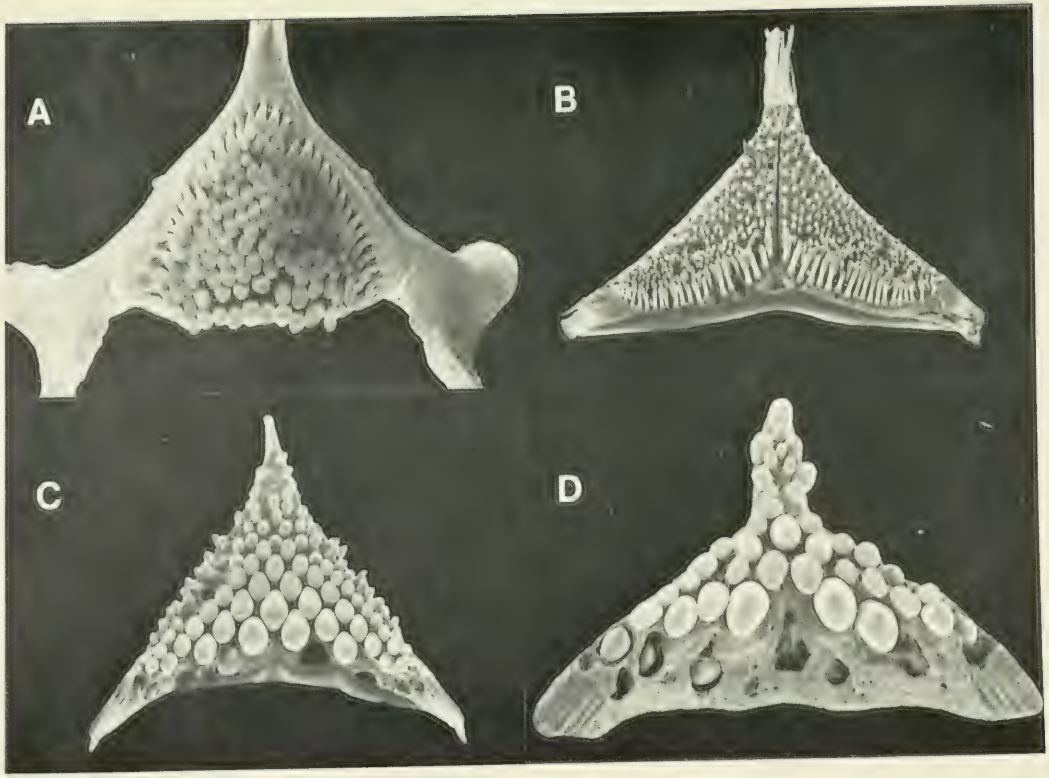


Figure 3. Scanning electronmicrographs of lower pharyngeal jaws of Labroidei (anterior is up on the page). A) Pomacentridae: *Pomacentrus littoralis*, a Pacific coral reef fish; B) Cichlidae: *Hemitilapia oxyrynchus*, from Lake Malawi, East Africa; C) Embiotocidae: *Cymatogaster aggregata*, from the pacific coast of North America; D) Labridae: *Tautoga onitis*, from the Atlantic coast of North America.

on the dorsal aspect of the fourth epibranchials (Liem, 1974). However, the pomacentrid LE_4 (Fig. 2A,B,D) splits near its insertion site on the fourth epibranchial (EB_4). The larger head inserts near the insertion site of LP, while a smaller medial head joins an oblique aponeurosis that runs anteromedially along the border of EB_4. The obliquus posterior (OP) is the major muscle operating the posterior region of the LPJ. The OP muscle runs between the broad dorsal flange of each muscular process and the flange along the EB_4 just below the insertion site of LE_4 (Fig. 2A, B, D). Here the LE_4 and OP muscles are separated by the oblique aponeurosis. Thus the sites of origin and insertion for OP in pomacentrids are the same as the other acanthopterygians, but the extremely close relationship between LE_4 and OP on the fourth epibranchial is a derived character. The aponeurosis is present in all pomacentrids examined, and it clearly separates the fibers of the LE_4 from those of the OP. Nevertheless, the insertions for the two muscles are extremely close together, a condition which seems to foreshadow the muscular sling of cichlids and other Labroidei. There is a broad flange on EB_4 to receive LE_4, and the posterior flanges on EB_4 and the fifth ceratobranchial (CB_5) are vertically aligned. Between them, and possibly contributing to the mechanical linkage between the two, is the stout dorsal portion of CB_4. Thus, while the muscles of the LPJ in pomacentrids still originate and insert on the same bones as in non-labroid acanthopterygians, the geometry of these insertions has been modified in a characteristic fashion. The resulting condition may represent a primitive counterpart to the cichlid muscular sling (Liem, 1974).

Synapomorphies Characterizing the Cichlidae

Six characters clearly distinguish the Cichlidae as a monophyletic assemblage: (1) The transversus dorsalis muscle is subdivided into four parts (Liem and Greenwood, 1981; Fig. 2E:TDA). (2) The premaxillae and maxillae of all cichlids are functionally decoupled; i.e., premaxillary protrusion can be regulated independently from motion of the maxillae by means of multiple mechanical pathways (Liem, 1978, 1979). Four additional characters have been described by Stiassny (1981): (3) There is an extensive cartilaginous cap on the anterior border of EB_2 (*Cichla ocellaris* being the exception). (4) Microbranchiospinae of characteristic form are present on the outer

faces of the second, third, and fourth gill arches. (5) The A_2 and A_ω portions of the adductor mandibulae complex have lost a major structural association, and there is an insertion of a large ventral division of A_2 onto the angulo-articular. (6) The head of EB_4 is distinctly expanded.

Synapomorphies Characterizing the Embiotocidae

Two characters are considered synapomorphies for the Embiotocidae. (1) All embiotocids are fully viviparous fishes, which deliver large, well-developed young. The males have a small intromittent organ derived from anal fin rays. The young are usually closely packed in the ovarian sacs which function in the fashion of a uterus. Monophyly of the embiotocids can be established on the basis of the highly specialized mode of "intra-uterine" development with its associated structural, physiological, and behavioral features, involving spatulate extensions of the webs of median and caudal fins, each with a rich blood supply (Webb and Brett, 1972). (2) Stiassny (1981) has found a small sheet of parallel muscle fibers arising from the anteromedial region of the A_1 part of the adductor mandibulae muscle and inserting upon the dorsal aponeurosis of A_{2+3} part of this muscle.

Synapomorphies Characterizing the Labridae

The families Labridae, Odacidae, and Scaridae have been recognized as close relatives within the Labroidei (Greenwood *et al.*, 1966). Here the three groups are recognized as a single family, the Labridae, since the monophyletic nature of this assemblage is strongly indicated by both morphological and functional characters. (1) The levator posterior muscle (Fig. 2C:LP) is the dominant muscle of the LPJ, forming a force couple with the pharyngocleithralis externus muscle (Liem and Greenwood, 1981). (2) The toothplates of the fourth pharyngobranchials are absent (either lost or fused with pharyngobranchial 3; Stiassny, 1981), while the first pharyngobranchials are absent or reduced. (3) The fourth epibranchials are highly modified and of characteristic form, articulating with the upper pharyngeal jaws (Yamaoka, 1978, 1980; Gobalet, 1978). (4) There is some form of physical contact between the LPJ and the cleithrum in all members of the clade (Liem and Greenwood, 1981).

The posterior face of the muscular process on each side of the LPJ bears an articular facet, which fits against a small fossa on the cleithrum. The mechanics of this joint are quite complex. Cineradiography of the LPJ in *Tautogolabrus adspersus* during mastication shows that there is a biphasic pattern involving both a hingelike and a sliding movement. The dynamics are reminiscent of those in the human temporo-mandibular joint. At rest and during the bite the LPJ is in close contact with the cleithrum and exhibits the pattern of a hinge-joint. During protraction the LPJ slides down and forward, using the anterior face of the cleithrum as a track. The morphology of the pharyngocleithral joints of odacids and scarids is basically similar to that of labrids, though the support system is stronger, and it is unknown whether the LPJ disarticulates during protraction. The condition in odacids and scarids overlaps broadly with that of the Labridae. *Cryptotomus roseus* is a scarid with a labridlike LPJ; both it and *Nicholsina denticulata* have many wrasselike features (see Gobalet, 1980 for comparative discussion of *Nicholsina*). *Pseudodax mollucanus* is a labrid with a scaridlike LPJ (Bleeker, 1862).

Interrelationships Among the Labroidei

The relationships proposed here differ from those of previous investigators (Greenwood *et al.,* 1966; Nelson, 1967; Liem and Greenwood, 1981) in three important ways. The Pomacentridae is considered the primitive sister group of other Labroidei. The Embiotocidae is postulated to be the sister group of the Labridae, and not the Cichlidae. Finally, the Labridae, Scaridae, and Odacidae are united in a single family, Labridae, to reflect striking similarities in their morphological as well as functional specialized features (Fig. 1).

Chief evidence for the proposed primitive sister-group relationship of the Pomacentridae to other Labroidei is found in the osteology and myology of the LPJ. In the Cichlidae, Embiotocidae, and Labridae, the LE_4 and (in general) LP muscles insert on the LPJ. The LE_4 and LP muscles of Pomacentridae insert on the fourth epibranchials, which represents the primitive condition in the Perciformes. Aerts and Verraes (1982) have demonstrated that the LE_4 of the cichlid *Haplochromis elegans* (and presumably, other cichids as well) is actually a composite of LE_4 plus a large medial head of the obliquus posterior muscle, the two fusing during

development. This condition is never fully developed in Pomacentridae (Fig. 2A, B, D: OP, LE_4). Obliquus posterior (OP) is the dominant muscle to the LPJ while LE_4 remains a separate muscle, though it is large, and is aligned with the OP. The result is that the two muslces together bridge the gap between prootic and LPJ, meeting across the fourth epibranchial, where they are separated by an aponeurosis (Fig. 2A, B, D: OP, LE_4).

Four derived characters establish sister-group relationship between the Embiotocidae and Labridae. (1) These groups have lost the second pharyngobranchial toothplates (Nelson, 1967; Stiassny 1981). (2) The first three branchial adductor muscles cover the anterodorsal faces of the epibranchials (Stiassny, 1980 and Fig. 2C, F: AD_{1+2}). (3) A ligament connects the postmaxillary process of the maxilla with the anterior border of the palatine and ectopterygoid (Stiassny, 1980). (4) Tooth rows are arranged radially across the LPJ, with teeth located directly over the symphysis between left and right fifth ceratobranchials. The LPJ toothplate is composed of two fields: an anterior field (often lost in durophages), and a posterior field bearing the large cardinal teeth used in crushing or grinding. New cardinal teeth are added only to the rear margin of the LPJ, forming a conveyor-like pavement with greatest wear toward the front (Fig. 3; see also Embiotocidae: *Damalichthys vacca;* Labridae: *Pseudodax mollucanus;* all scarids).

The phylogeny proposed in Figure 1 assumes that similarities in pharyngeal dentition between the Labridae and Embiotocidae on the one hand, and Pomacentridae on the other, are homoplasies. In cichlids the LPJ toothplate is divided into left and right regions, with the largest teeth arranged in two main rows parallel to the symphysis, and there are no teeth located directly over the symphysis. This is clearly the primitive condition, since (a) the LPJ of labroids is derived from two separate fifth ceratobranchial bones, and (b) this condition is displayed in those non-labroid perciforms possessing fused or joined fifth ceratobranchials. In pomacentrids, as well as in embiotocids and labrids, the teeth cross the plate in a radial series and there are teeth located directly over the symphysis. As a sole synapomorphy for pomacentrids, embiotocids, and labrids this character seems too tentative. It appears independently in the Beloniformes, another group with fused lower pharyngeal jaws, which is clearly unrelated to the Labroidei (Collette, 1966). Pharyngocleithral joints appear in both the Pomacentridae and the

Labridae, but are clearly dissimilar in form. Thus in terms of the specialized osteological and myological characters discussed above, the pharyngeal jaws of the Cichlidae, Embiotocidae, and Labridae resemble each other much more closely than any one of these groups resembles the Pomacentridae.

Independent investigations (Stiassny, 1981; Liem and Greenwood, 1981, and this study) have resulted in very similar hypotheses of labroid phylogenetic relationships. Stiassny (1981, personal communication) has based her studies primarily on soft-tissue characters, while we have concentrated on functional and osteological characters. The relationships postulated in Figure 1 deviate drastically from previous schemes. This is mainly because important new osteological, dental, and myological evidence has emerged.

DISCUSSION

Ecology of the Labroidei

The new phylogenetic scheme of the Labroidei has important implications for our perception of the ecology and functional morphology of this group. The gradal nature of former classifications obscures relationships and thereby masks evolutionary sequences, ecological diversity, and changes in functional patterns. To illustrate this point we will briefly discuss some of the implications of the new phylogeny for ecological concepts as they pertain to the Labroidei.

Labroidei as defined here unites at least 1,470 species (some 5 to 10 percent of living fishes) that are extremely diverse ecologically. Nevertheless, the majority of labroids occur within one general type of environment: warm, slow-moving water with abundant habitat structure. Tropical marine reefs are densely populated by pomacentrids and labrids. These are joined by embiotocids on temperate Pacific reefs. All four clades figure prominently in aquatic macrophyte forests such as grass beds, kelp beds, algal reefs, or heavily vegetated pond and stream edges. Relatively few labroids are abundant in pelagic, soft-bottom, or strictly lotic assemblages.

Modes of life exhibited by marine labroids differ characteristically from those of sympatrically occurring non-labroid and functionally intermediate forms. We illustrate these patterns with data from a coral reef fish assemblage observed in Salt River Canyon, St. Croix, U.S. Virgin Islands (Table 1). The 137 species

Table 1. Relationship between functional morphology of the pharyngeal jaws and potential anti-predator mechanisms for 137 species of coral reef fishes observed during visual censuses in Salt River Canyon, St. Croix, U.S. Virgin Islands (Kaufman and Ebersole, in preparation).

Potential Anti-Predator Mechanisms	Functional Morphology of Pharyngeal Jaws		
	Primitive	Intermediate	Labroid
Non-territorial	O = 52	O = 10	O = 5
Non-schooling	E = 33.74	E = 18.09	E = 15.16
Not heavily armed	X^2 = 9.88	X^2 = 3.62	X^2 = 6.81
	O = 16	O = 17	O = 0
Heavily armed	E = 16.62	E = 8.91	E = 7.47
	X^2 = 0.02	X^2 = 7.35	X^2 = 7.47
Territorial or	O = 1	O = 10	O = 26
Schooling	E = 18.64	E = 9.99	E = 8.37
Not heavily armed	X^2 = 16.69	X^2 = 0.00	X^2 = 37.13
	$X^2 = 88.98$, $p < .001$		

O = observed frequencies for numbers of species in each category.
E = expected frequencies.
X^2 = Chi-square value within cell.
X^2 = total Chi-square.

observed during two series of replicated visual censuses (Kaufman and Ebersole, in preparation) were divided into three categories according to pharyngeal jaw functional morphology: (1) primitive, with pharyngeal jaws unspecialized for mastication; (2) intermediate forms exhibiting some, but not all of the features found in Labroidei (as discussed below in greater detail); and (3) labroids. The species were also placed into three other categories related to strategies for avoiding predation (refuging): (1) non-territorial and non-habitually schooling species, both unarmed; (2) strongly territorial and habitually schooling species, both unarmed; and (3) species armed with frank defensive mechanisms (toxin, venom, dermal armor, enlarged spines), or which live inside corals, sponges, invertebrate tests, and boreholes. It was postulated that trophic mechanisms and refuging strategies would be interrelated. Table 1 provides evidence of highly significant relationship between "pharyngeal jaw" and "anti-predation" categories ($X^2 = 88.98$; $p < .001$). A detailed list of the species and their categorizations can be obtained from the authors.

The data in Table 1 suggest that there are characteristic modes of life for coral reef labroids. Most of them both feed and refuge on the reef. They are not heavily armed. They are, for the most part, either territorial or schooling. Territorial labroids defend a general area as a multipurpose territory rather than occupying one specific hole or cavity as do many inquiline gobies, blennies, or jawfishes (Opisthognathidae). The residents exclude potential competitors for food, hiding places, and mates, as well as species that threaten the integrity of the territory (Low, 1971; Thresher, 1976; Kaufman, 1977, 1979; Potts, 1977; Williams, 1979, 1980; Ebersole, 1977; Lobel, 1980). Even the schooling and planktivorous labroids are strongly reef-associated, utilizing benthic cover as the ultimate means of escape from predators. In summary, members of the Labroidei generally rely on the reef for refuge, exploiting those foods which are, or can be made available without travelling over long distances. There is an exception to this pattern. Adults of the larger species (such as the huge Caribbean parrotfishes *Scarus guacamaia* and *S. coelestinus*) sometimes forage or migrate to and from the reef as individuals. For these fishes, large size alone may be a sufficient deterrent against predators.

Other reef-dwelling fishes exhibit modes of life that contrast with those of the labroids. The non-labroid category in Table 1, including such fishes as berycoids, apogonids, serranids, and lutjanids, consists of both diurnal and nocturnal predators which stalk small soft-bodied prey. The intermediate pharyngeal jaw category is dominated by two groups: armed fishes that feed on the reef by day and rest on the reef at night, and unarmed fishes that feed off-reef at night and shelter on the reef during the day. The heavily armed plectognaths, chaetodontids, and acanthurids comprising the bulk of the first group together exploit almost as broad a range of foods as the labroids. Individually, however, they exhibit functional limitations related to gape, mouth position, jaw mobility and pharyngeal jaw mechanics that should seriously limit feeding versatility in comparison to that of similar-sized pomacentrids or labrids. This is reflected in what is known of their diet (e.g., Randall, 1967; Hobson, 1974; Reese, 1975). Relatively few of these species enhance their own local food supply by defending feeding territories (possibly *Acanthurus sohal,* Vine, 1974; *Chaetodon trifascialis* [formerly *Megaprotodon strigangulus*], Reese, 1975). The nocturnal

off-reef predators (e.g., Pomadasyidae) prey chiefly on small benthic invertebrates.

We postulate that feeding versatility was a chief factor in shaping the characteristic modes of life exhibited by marine labroids; i.e., schooling or territorial behavior with a strong reliance on the reef for both food and shelter. Trophic mobility can be one key to survival when spatial mobility is limited by a high risk of predation. The antithesis of this strategy, rarely exhibited by labroids, is to reduce the risk of predation by adopting some active defensive mechanism.

Labroids play a disproportionate role in determining the distribution and abundance of benthic organisms in tropical marine hard-bottom communities (Randall, 1961, 1974; Ogden and Lobel, 1978; Brock 1979). In part this is due to broad-spectrum feeding capabilities (hard-shelled invertebrates, coral rock, coral, algae). Many labroids locally manipulate the substratum and its occupants to suite their own needs (Brawley and Adey, 1977; Kaufman, 1977, 1979; Wellington, 1981). This constitutes a patchy disturbance to sessile invertebrates (Kaufman, 1977; Connell, 1978) and could be a principal factor regulating food abundance for other reef organisms.

Labroid Phylogeny and the Evolution of Acanthopterygian Feeding Mechanisms

When the cichlid pharyngeal jaw mechanism was first described, it appeared to represent an abrupt breakthrough in the acanthopterygian feeding mechanism, radically different from anything known in the cichlids' presumed ancestors (Liem, 1974). Subsequent radiation seemed to involve little modification of the basic feeding mechanism (Fryer and Iles, 1972; Greenwood, 1974). The new hypothesis on the genealogical relationships of the Labroidei presented here requires that these views be revised considerably.

One erroneous hypothesis was that the pharyngeal jaw complex is unique to cichlids; present evidence rejects such a hypothesis (Liem and Greenwood, 1981). Many features present in cichlids are present in Labroidei. Second, there was thought to be a large morphological and functional gap between cichlids and their primitive (ancestral) counterparts; there is not. The apparent gap was an artifact of insufficient data, now bridged by primitive labroids and certain non-labroid perciforms. Aerts and Verraes (1982) have shown that during the ontogeny of a cichlid (*Astatoti-*

lapia elegans) the LE_4 splits into a lateral and a medial head. The medial head of LE_4 unites with the medial head of the OP, thus establishing a functionally as well as a structurally uninterrrupted muscle between the prootic and the muscular process of the LPJ, i.e., a compound LE_4. The characteristic arrangement of LE_4 and OP in pomacentrids (e.g., *Pomacentrus littoralis,* Fig. 2) resembles those early ontogenetic stages in cichlids before the compound muscle is formed. The Pomacentridae is clearly primitive, however, in terms of the origins and insertions of LE_4 and OP. Thus the Pomacentridae is intermediate between the more derived labroids (cichlids, embiotocids, and labrids) and other perciforms.

Other perciforms which approach the labroid condition in one or more respects are morphologically (and perhaps phylogenetically) intermediate between labroids and primitive perciforms. The anabantoids, Kyphosidae, and Sciaenidae have fused or joined pharyngeal jaws in some members. The fifth ceratobranchials of the Gerreidae and Pomadasyidae (especially *Anisotremus surinamensis*) have no true bony junction, but are in some species very tightly bound together by strong ligaments. Certain Sciaenidae (e.g., *Pogonias chromis, Aplodinotus grunniens*) and Gerreidae have an articulation between the upper pharyngeal jaws and the basicranium although it is not as well developed as in labroids. The shell-cracker centrarchid *Lepomis microlophus* and the molluscivorous Carangidae (*Trachinotus* spp.) have broad, hypertrophied lower pharyngeal jaw elements which meet closely at the midline (Kaufman and Ono, in preparation). Nearly all of these morphologically intermediate forms feed habitually on hard-shelled benthic invertebrates in addition to a wide variety of other organisms, both hard and soft. Selection favoring a broader, more inclusive diet could have been a major factor in the early evolution of labroids. This hypothesis can not be tested without first developing a better picture of perciform phylogeny. However, the presence of so many intermediate forms (one of which may represent the primitive sister group of the Labroidei) and the intermediate characteristics displayed in Pomacentridae, indicate that advanced acanthopterygian pharyngeal jaws are the result of a series of morphological changes. There was no single "adaptive breakthrough" (*sensu* Simpson, 1944, 1953; Liem, 1974).

In summary, this new model of labroid relationships will permit us to examine the nature of evolutionary change in a structurally complex mechanical system. Judging from the great ecological diversity of labroids, it seems that their specialized pharyngeal jaw apparatus has greater structural potential and functional flexibility than that of its more primitive counterparts. The more precise labroid phylogenetic scheme will allow us to determine if there is a general relationship between design versatility and historical patterns of morphological change.

ACKNOWLEDGMENTS

We owe much to the useful comments made by William and Sara Fink, Humphry Greenwood, and Dana Ono. Melanie Stiassny contributed generously from her own observations on labroid systematics. Karsten Hartel aided in locating study material. Ed Seling and Al Coleman assisted in electron microscopy and photography. William B. Hamner, Jr. made important contributions to studies of the pharyngeal jaw in labrids, and helped in collecting specimens; William McFarland contributed many embiotocid specimens. We thank the staffs of the West Indies Marine Laboratory and the Discovery Bay Marine Laboratory for assistance in specimen collection and field observations. This work was supported by National Science Foundation Grant DEB-79-00955 to K. Liem; National Oceanographic and Atmospheric Administration Grant NULS-1 Mission 81-8 to L. Kaufman and J. Ebersole; and National Science Foundation Grant OCE 79-12674 to J.B.C. Jackson. This paper is contribution No. 261 from the Discovery Bay Marine Laboratory, Discovery Bay, Jamaica, W.I.

LITERATURE CITED

Aerts, P., and W. Verraes. 1982. The development of the musculus levator externus IV and the musculus obliquus posterior in *Haplochromis elegans* Trewavas, 1933 (Teleostei: Cichlidae): a discussion on the shift hypothesis. J. Morphol., in press.

Bleeker, P. 1862. Atlas ichthyiologique des Inde Orientales Neerlandaises. Amsterdam: De Breuk & Smits á Leyde, Vol. I., 168 pp.

Brawley, S. H., and W. H. Adey. 1977. Territorial behavior of the threespot damselfish (*Eupomacentrus planifrons*) increases reef algal productivity. Environ. Biol. Fish., 2: 45–51.

Brock, R. E. 1979. An experimental study of the effect of grazing by parrotfishes and role of refuges in benthic community structure. Mar. Biol., **51**: 381–388.

Collette, B. B. 1966. *Belonion,* a new genus of fresh-water needlefishes from South America. Am. Mus. Novitates, No. 2274, pp. 1–22.

Connell, J. H. 1978. Diversity in tropical fish forests and coral reefs. Science, **199**: 1302–1310.

Ebersole, J. P. 1977. The adaptive significance of interspecific territoriality in the reef fish *Eupomacentrus leucostictus.* Ecology, **58**: 914–920.

Fryer, G., and T. D. Iles. 1972. The cichlid fishes of the great lakes of Africa. Edinburgh, Oliver and Boyd, 641 pp.

Gobalet, K. W. 1980. Functional morphology of the head of parrotfishes of the genus *Scarus.* Ph.D. Dissertation, University of California, Davis, 224 pp.

Greenwood, P. H. 1974. The cichlid fishes of Lake Victoria, East Africa: The biology and evolution of a species flock. Brit. Mus. (Nat. Hist.) Bull. Suppl. No. 6, 134 pp.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman, and G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist., **131**(4): 345–354.

Hobson, E. S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., **72**: 915–1031.

Hutchinson, G. E. 1958. Concluding remarks, Cold Spring Harbor Symposium. Quant. Biol., **2**: 415–427.

———. 1965. The niche: an abstractly inhabited hypervolume, pp. 26–78. *In* The Ecological theatre and the evolutionary play, New Haven, Yale University Press.

Kaufman, L. 1977. The threespot damselfish: Effects on benthic biota of Caribbean coral reefs. Proc. Third Int. Coral Reef Symp., **1**: 559–564.

———. 1979. Damselfish gardens on Caribbean reefs: a natural disturbance and its effects on benthic biota. Ph.D. Dissertation, Johns Hopkins University, Baltimore, MD, 140 pp.

Liem, K. 1974. Evolutionary strategies and morphological innovations: Cichlid pharyngeal jaws. Syst. Zool., **22**: 425–441.

———. 1978. Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. I. Piscivores. J. Morphol., **158**: 323–360.

———. 1979. Modulatory multiplicity in the feeding mechanism in cichlid fishes, as exemplified by the invertebrate pickers of Lake Tanganyika. J. Zool. Soc. Lond. **189**: 93–125.

———. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. Amer. Zool., **20**: 295–314.

———. 1982. Functional versatility, speciation, and trophic niche overlap: are fishes different? *In* D. Meyers, and R. Strickler (eds.), Trophic Dynamics in Aquatic Ecosystems. AAAS selected symposia, in press.

Liem, K. F., and P. H. Greenwood. 1981. A functional approach to the phylogeny of the pharyngognath teleosts. Amer. Zool., **21**: 83–101.

Liem, K. F., and J. W. M. Osse. 1975. Biological versatility, evolution and food resource exploitation in African cichlid fishes. Amer. Zool., **15**: 427–454.

Lobel, P. S. 1980. Herbivory by damselfishes and their role in coral reef community ecology. Bull. Mar. Sci., **30**: 273–289.

Low, R. M. 1971. Interspecific territoriality in a pomacentrid reef fish, *Pomacentrus flavicauda* Whitley. Ecology, **52**: 648–654.

Nelson, G. J. 1967. Gill arches of some teleostean fishes of the families Girellidae, Pomacentridae, Embiotocidae, Labridae, and Scaridae. J. Nat. Hist., **1**: 289–293.

Ogden, J. C., and P. S. Lobel. 1978. The role of herbivorous fishes and urchins in coral reef communities. Environ. Biol. Fish., **3**: 49–63.

Potts, D. C. 1977. Suppression of coral population by filamentous algae within damselfish territories. J. Exp. Mar. Biol. and Ecology, **28**: 207–216.

Randall, J. E. 1961. Overgrazing of algae by herbivorous marine fishes. Ecology, **42**: 812.

———. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Ocean., Univ. of Miami, (5): 665–847.

———. 1974. The effect of fishes on coral reefs. Proc. Second Int. Coral Reef Symp., 1: 159–166.

Reese, E. S. 1975. A comparative field study of the social behavior and related ecology of reef fishes of the family Chaetodontidae. Z. Tierpsychol., **37**: 37–61.

Simpson, G. G. 1944. Tempo and Mode in Evolution. New York, Columbia Univ. Press, 237 pp.

———. 1953. The Major Features of Evolution. New York, Columbia Univ. Press, 434 pp.

Stiassny, M. L. J. 1980. The anatomy and phylogeny of two genera of African cichlid fishes. Ph.D. Dissertation, University of London.

———. 1981. The phyletic status of the family Cichlidae (Pisces: Perciformes): A comparative anatomical investigation. Neth. J. Zool., **31**: 275–314.

Taylor, W. R. 1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus., **122**(3596): 1–17.

Thresher, R. E. 1976. Field analysis of the territoriality of the threespot damselfish, *Eupomacentrus planifrons* (Pomacentridae). Copeia, **1976**: 266–276.

Vine, P. J. 1974. Effects of algal grazing and aggressive behavior of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral reef ecology. Mar. Biol., **24**: 131–136.

Webb, P. W., and J. R. Brett. 1972. Respiratory adaptations of prenatal young in the ovary of two species of viviparous seaperch *Rhacochilus vacca* and *Embiotoca lateralis*. J. Fish. Res. Bd. Canada, **29**: 1525–1542.

Wellington, G. M. 1981. The role of competition, niche diversification and predation on the structure and organization of a fringing coral reef in the Gulf of Panama. Ph.D. Dissertation, University of California, Santa Barbara.

Williams, A. H. 1979. Interference behavior and ecology of the threespot damselfish. Oecologia, **38**: 223–230.

———. 1980. The threespot damselfish: a noncarnivorous keystone species. Amer. Natur., **116**: 138–142.

Yamaoka, K. 1978. Pharyngeal jaw structure in labrid fish. Publ. Seto. Mar. Biol. Lab., **24**: 409–426.

———. 1980. Some pharyngeal jaw muscles of *Calotomus japonicus* (Scaridae, Pisces). Publ. Seto. Mar. Biol. Lab., **25**: 315–322.

LIBRARY
MAR 1 8 1985
HARVARD UNIVERSITY

B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 29 APRIL 1983 NUMBER 473

THE INTERRELATIONSHIPS OF PELYCOSAURS

DONALD BRINKMAN[1] AND DAVID A. EBERTH[2]

ABSTRACT. An analysis of 17 characters forms the basis of a hypothesis of relationships of seven pelycosaur genera. These genera include representatives from most of the higher taxa recognized by Romer and Price (1940). In agreement with the phylogeny proposed by Romer and Price, *Edaphosaurus* is considered to be more closely related to *Dimetrodon* than is *Ophiacodon*. In contrast to the phylogeny proposed by Romer and Price, *Ophiacodon* is considered more closely related to *Dimetrodon* than are *Varanops* and *Aerosaurus*. Three character-states that are interpreted as being derived are shared by *Casea*, *Varanops*, and *Aerosaurus*, suggesting that these three genera are members of a clade distinct from the clade including *Ophiacodon*, *Edaphosaurus*, and *Dimetrodon*.

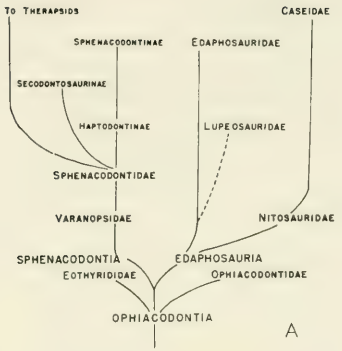
INTRODUCTION

Pelycosaurs occupy a central position in amniote evolution. As a paraphyletic taxon within the clade including mammals, pelycosaurs have played an important role in considerations of the origin of mammals. Also, pelycosaurs include some of the most primitive known reptiles, and are an important element in consideration of the early evolution of amniotes. Thus, an understanding of pelycosaur interrelationships has implications for many broader problems of reptile diversification.

Pelycosaurs were the subject of a detailed monographic study by Romer and Price (1940), and as a result are one of the best understood groups of Paleozoic reptiles. Romer and Price used evolutionary systematics in their study of pelycosaurs (Fig. 1A). In line

[1]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. Present Address: Tyrrell Museum of Paleontology, Box 7500, Drumheller, Alberta, Canada, TOJ OYO.

[2]Department of Geology, University of Toronto, Toronto, Ontario, Canada, M5T 1R7.



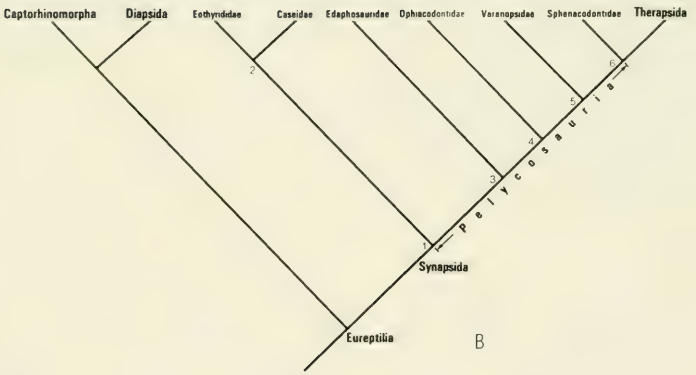


Figure 1. Hypotheses of pelycosaur interrelationships. A) Phylogeny of pelycosaurs presented by Romer and Price (1940); B) Cladogram showing the interrelationships of pelycosaurian families presented by Reisz (1980). A is from Romer and Price, 1940; B is from Reisz, 1980.

with this approach, taxa were established on the basis of phenetic similarity. This is reflected in the diagnoses, which consist of generalized descriptions that encompass the anatomy of most of the members of the group. The taxonomic rank assigned to a group was based on both the diversity within the assemblage and the morphological distance between that and other groups. Ecological interpretations also played a significant role in their study of pelycosaur evolution, and a scenario uniting the morphological and ecological interpretations was developed.

Some aspects of the phylogeny proposed by Romer and Price were brought into question by Langston (1965), who proposed a close relationship between *Oedaleops* and *Eothyris,* and argued that these genera were close to the ancestry of caseids. This implied that caseids were not closely related to the edaphosaurids, as was suggested by Romer and Price.

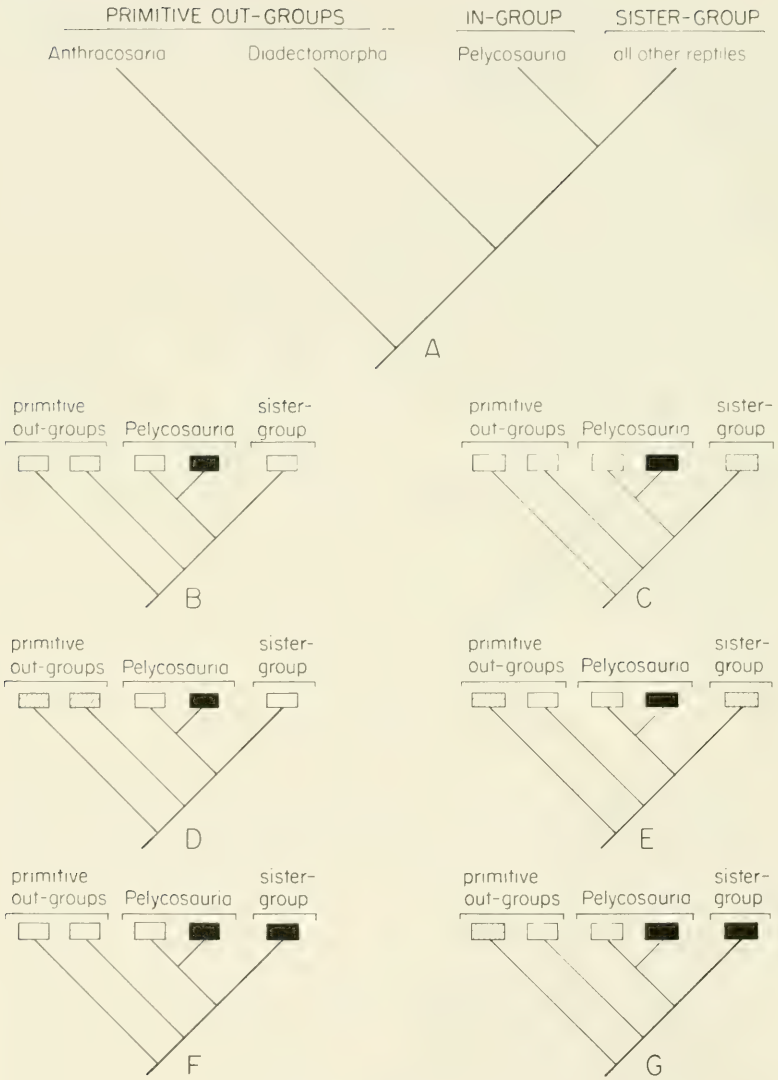
Recently, Reisz (1980) reviewed pelycosaur interrelationships using a cladistic analysis of the characters available to Romer and Price. Reisz concluded that many of the families recognized by Romer and Price were monophyletic, but the interrelationships of the families that Reisz proposed (Fig. 1B) differed from those suggested by Romer and Price. Also, the relationships that Reisz recognized did not conform to the scenario of pelycosaur evolution proposed by Romer and Price.

During the study of a new pelycosaur from El Cobre Canyon, New Mexico, it became clear that much additional morphological information could be brought to bear on the problem of pelycosaur interrelationships, and a review of the group was undertaken. The results of this review are intended to provide a testable hypothesis of pelycosaur interrelationships, and to serve as a framework in which detailed taxonomic and morphological revisions of individual genera and families can be interpreted.

MATERIALS AND METHODS

The central problem in a cladistic analysis is establishing the polarity of character-states. Out-group comparison has been considered the most powerful tool for this (Watrous and Wheeler, 1981). The interrelationships of the groups used in determining the polarity of character-states within pelycosaurs are shown in Figure 2A. These relationships are based on Carroll (1970), except for the position of *Diadectes,* which, following Heaton (1980), is placed with *Limnoscelis* and *Tseajaia* in the Diadectomorpha. Also, following Kemp (1980), pelycosaurs are considered to be the sister-group of all other reptiles.

In using out-group comparison to interpret polarities, two principles are used. One is the principle of parsimony: the hypothesis of polarities that requires the least number of evolutionary events to account for the distribution of character-states will be accepted.


PRIMITIVE OUT-GROUPS
IN-GROUP
SISTER-GROUP
Anthracosaria
Diadectomorpha
Pelycosauria
all other reptiles
A
primitive out-groups
Pelycosauria
sister-group
B
C
D
E
F
G

This principle is the basis for the interpretation of polarities for the character-states whose distribution is shown in Figure 2B–E.

The second principle is the co-occurrence of primitive character-states. According to this principle, primitive character-states tend to occur together. Using this principle, the character-state that occurs in the outgroup that, on the basis of other evidence, is thought to be more primitive is accepted as the primitive character-state. This is the basis for the interpretation of polarities for the character-states whose distribution is shown in Figure 2F and G. It shoud be noted that implicit in this principle is the assumption that reversals are less likely to occur than are independent acquisitions. The use of this principle, therefore, limits the extent to which the results presented here can be used to test this assumption.

Characters of uncertain polarity will not be used to support relationships. However, such characters may provide corroboration of relationships proposed on the basis of derived character-states, since the distribution of uncertain character-states will be either consistent with the cladogram or will require that the occurrence of parallel evolution be hypothesized.

One of the problems in the study of the evolution of groups represented by fossil material is the incorporation of data both from well-known animals and from animals represented by incomplete specimens. This is especially true in the study of the evolution of early reptiles, where material is rare and, in many cases, animals are represented by single fragmentary specimens. Often animals represented by such material have been assigned to a taxon erected on the basis of well-known animals, and discussions of the evolution of the group have focused on the interrelationships of the higher taxa.

Figure 2. The interpretation of polarities of character-states by outgroup comparison. A) Cladogram showing the interrelationships of the taxa used as out-groups for interpreting the polarity of character-states within pelycosaurs; Diadectomorpha includes *Diadectes*, *Limnoscelis*, and *Tseajaia*; B–G) Interpretation of polarities of character-states. In B–E, this is based on parsimony, in F and G, this is based on the principle of co-occurrence of primitive character-states. ■ represent the derived in-group character-states; □ represent the primitive in-group character-states; ▨ represent character-states not present in the in-group.

In order that information from both fragmentary and well-known animals can be incorporated into the analysis of pelycosaur interrelationships, this study will be separated into two steps. The first will be to construct a cladogram showing the interrelationships of the most completely known genera using all available morphological features. This will provide a framework in which data from the less well known genera can be interpreted. The results of this part of the study are presented here. The second part will be the inclusion of the less well known animals in the analysis. Through this, the cladogram will be tested and a more detailed understanding of pelycosaur interrelationships will be obtained.

By using genera as the basis for considering pelycosaur interrelationships, all morphological diversity known to be present within higher taxa will be incorporated in a single analysis of diversification of pelycosaurs. Also, assumptions about pelycosaur evolution are minimized. Some currently recognized higher taxa are almost certainly monophyletic and could be treated as units in a discussion of pelycosaur interrelationships. Others, such as the Ophiacodontidae, as currently defined may be either polyphyletic or paraphyletic. By treating each genus as an independent entity, this potential source of error is avoided.

The pelycosaurs considered here are *Casea, Varanops, Aerosaurus, Ophiacodon, Edaphosaurus, Dimetrodon,* and *Sphenacodon.* The restriction of the study to these genera was necessitated by the accessibility of material for direct observation and the fragmentary nature of available specimens of other genera. Only characters that were actually observed were utilized in the analysis, and many of the reconstructions presented here are modified from previously published reconstructions on the basis of observations made during the course of this work. This required that a large amount of material be examined, and supplying a complete list of specimens studied is not possible. To facilitate future work, the specimens that showed particular structures most clearly are listed in Table 1, and the specimens that are the basis for the modifications in the reconstructions are listed in the figure legends. In all the features considered here, *Sphenacodon* and *Dimetrodon* are indistinguishable (Eberth, 1981). Thus, illustrations from only one of these genera are included here.

Table 1. List of specimens preserving the structures described in the text.

Character	*Casea*	*Varanops*	*Ophiacodon*	*Edaphosaurus*	*Dimetrodon*
Supraoccipital	UC 698	——	MCZ 1366	MCZ 1762	MCZ 1347
Tabular	UC 698	——	MCZ 1426	MCZ 1762	MCZ 1347
Basipterygoid tubercula	UR 1011	——	MCZ 4920	MCZ 1531	MCZ 1697
Stapes	UC 698	P 12841	MCZ 1350	MCZ 1762	MCZ 1347
Quadrate ramus of pterygoid	UC 698	P 12841	MCZ 1350	MCZ 1762	MCZ 5950
Basisphenoid shelf	UC 698	UR 2423	MCZ 4820	MCZ 1531	MCZ 1697
Frontal	UC 656	UR 2423	MCZ 1366	MCZ 4309	MCZ 4430
Maxilla	UC 698	UR 2423	MCZ 1366	MCZ 1762	MCZ 1347
Premaxilla	UC 698	MCZ 1926	MCZ 1366	MCZ 1680	MCZ 4982
Quadratojugal	UC 656	UR 2423	MCZ 1366	MCZ 1762	MCZ 6173
Pterygoideus process	——	MCZ 1926	MCZ 1203	MCZ 1370	MCZ 3244
Angular	UC 698	UR 2423	MCZ 1203	MCZ 1370	MCZ 7539
Vertebrae	UC 883	MCZ 1926	MCZ 5912	MCZ 1754	MCZ 5210
Humerus	UC 656	UR 695	MCZ 1486	MCZ 3417	MCZ 8708
Postparietal	UC 698	——	——	MCZ 1762	MCZ 1347
Paroccipital process	UC 656	UR 2423	MCZ 1426	MCZ 1762	MCZ 1347

Abbreviations: UC, UR, and P: specimens housed in the Field Museum of Natural History; MCZ: specimens housed in the Museum of Comparative Zoology.

CHARACTER ANALYSIS: I. FEATURES FOR WHICH POLARITY CAN BE INTERPRETED

Ventral Margin of Skull

In *Dimetrodon, Sphenacodon* (Fig. 3F), *Edaphosaurus* (Fig. 3E), and *Ophiacodon* (Fig. 3D), the ventral margin of the cheek region of the skull is concave (i.e, bowed upward).

In *Casea* (Fig. 3B), *Varanops* (Fig. 3C), and *Aerosaurus* (Langston and Reisz, 1981), the ventral margin is convex and extends below the level of the tooth row.

The ventral margin of the cheek is convex in *Limnoscelis* (Romer, 1946), *Diadectes* (Fig. 3A), and anthracosaurs (Panchen, 1970). In *Hylonomus,* the cheek margin is straight (Carroll, 1964). Thus, three character-states can be recognized: the presence of a concave ventral cheek margin, a convex ventral cheek margin, and a straight

ventral cheek margin. They have the distribution shown in Figure 2C, with the derived character-state present in pelycosaurs being the presence of a concave cheek margin. The condition seen in *Hylonomus* is a separate, derived character-state.

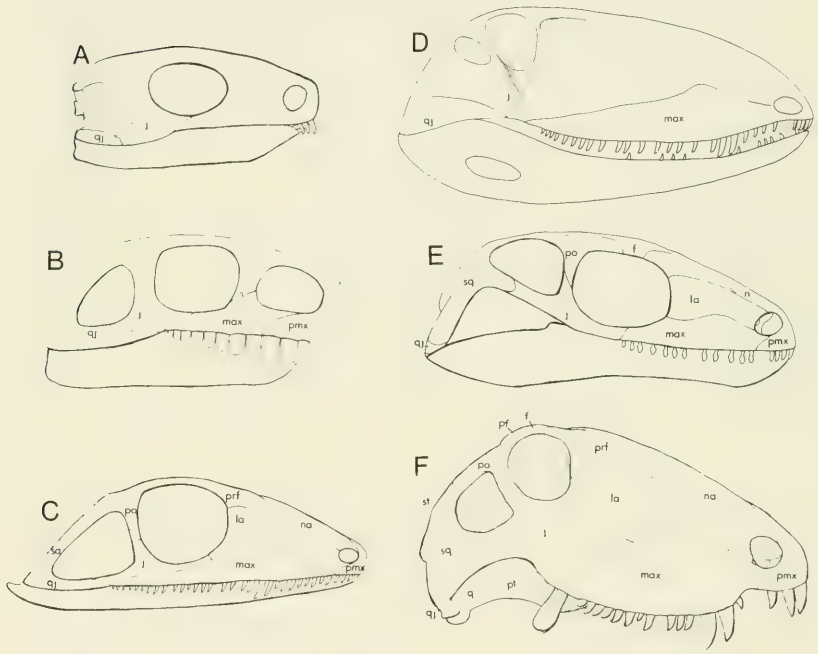


Figure 3. The skulls in right lateral view of A) *Diadectes;* B) *Casea;* C) *Varanops;* D) *Ophiacodon;* E) *Edaphosaurus;* and F) *Sphenacodon.* Drawing of *Diadectes* based on MCZ 1739, MCZ 1736, and MCZ 2086; *Casea* based on UC 698 and UC 656; *Varanops* based on MCZ 1926 and UR 2423; *Ophiacodon* based on UC 671; *Edaphosaurus* based on MCZ 1762, MCZ 1764, and USNM 299844; *Sphenacodon* from Eberth (1981).

Abbreviations: f, frontal; j, jugal; la, lacrymal; max, maxilla; na, nasal; pf, postfrontal; pmx, premaxilla; po, postorbital; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sq, squamosal; st, supratemporal.

Premaxilla

In *Dimetrodon, Sphenacodon* (Fig. 3F), *Edaphosaurus* (Fig. 3E), and *Ophiacodon* (Fig. 3D), the anterior margin of the premaxilla slopes posteriorly from the anterior termination of the tooth row giving a convex outline to the snout.

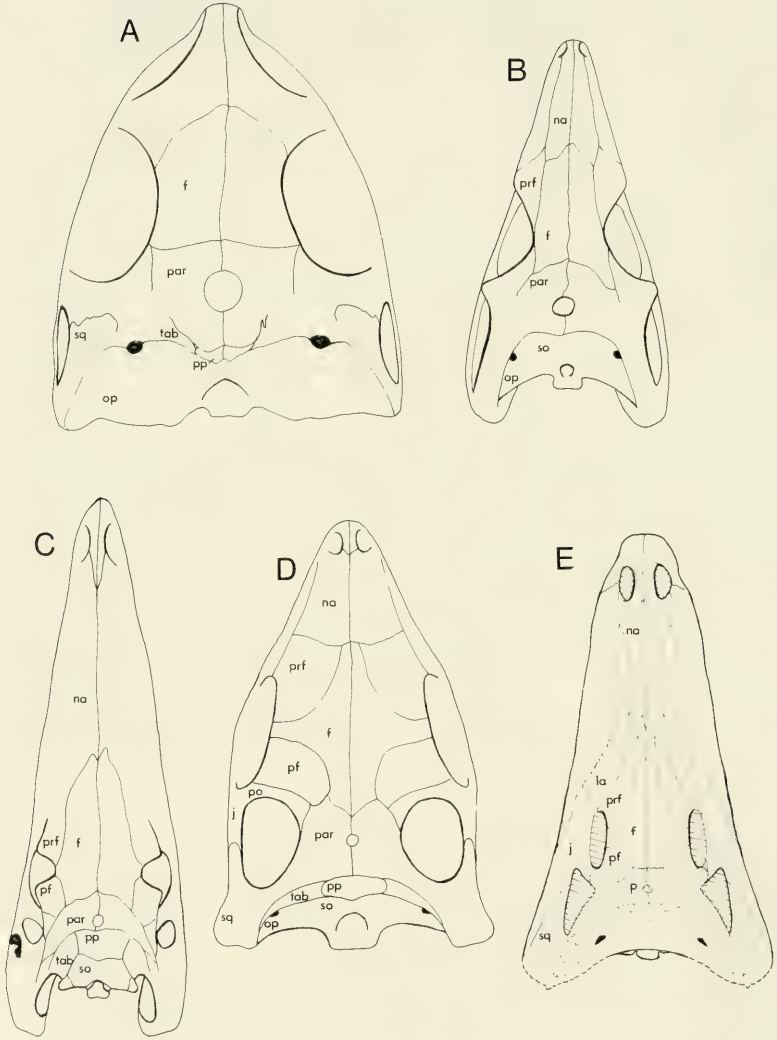
In *Casea* and *Varanops* (Fig. 3B–C), the anterior margin of the premaxilla first extends anteriorly from the anterior termination of the tooth row, giving a forwardly projecting rostrum. Langston and Reisz (1981) argue that the forward sloping premaxilla seen in *Aerosaurus* specimen UCMP 40096 is a result of displacement of the element, and they reconstruct the skull with a posteriorly sloping premaxilla. However, apart from the slope of the premaxilla, there is no direct evidence that the premaxilla has been displaced, and no evidence that the structure of this part of the skull was different than in *Varanops.*

In *Diadectes,* the dorsal process of the premaxilla is vertical (Fig. 3A). *Limnoscelis* is like *Varanops, Casea,* and *Aerosaurus* in having a forwardly projecting rostrum (Romer, 1946). Anthracosaurs, with an elongate, flattened face, are not directly comparable to either condition seen in pelycosaurs. The structure of the premaxilla in *Hylonomus* and *Paleothyris* is not known for certain. In *Romeria,* the dorsal ramus of the premaxilla is nearly vertical (Heaton, 1979), a condition not specifically similar to either of the character-states present in pelycosaurs. Thus, these character-states have the distribution shown in Figure 2E, with the presence of a forwardly sloping dorsal ramus of the premaxilla being the primitive condition.

Frontals

In *Dimetrodon* and *Sphenacodon* (Fig. 4E), the frontal has a laterally directed lappet that is greater in mediolateral width than is the posterior end of the frontal. *Edaphosaurus* was figured as having a broad flange extending laterally along the entire anterior half of the frontal by Romer and Price (1940). However, isolated frontals show that the lateral flange illustrated by Romer and Price is formed in part by the prefrontal, and that a lateral lappet like that of *Dimetrodon* and *Sphenacodon* is present (Fig. 4D).

In *Ophiacodon* (Fig. 4C), the frontal is without a strongly developed lateral lappet. A small projection extends between the base of


A
f
par
sq
tab
pp
op
B
na
prf
f
par
so
op
C
na
prf
f
pf
par
pp
tab
so
D
na
prf
f
pf
po
j
par
pp
tab
so
sq
op
E
na
la
prf
f
j
pf
p
sq

the prefrontal and postfrontal, but the width of this is much less than the width of the posterior end of the frontal.

In *Casea* (Fig. 4A), *Varanops* (Fig. 4B), and *Aerosaurus* (Langston and Reisz, 1981), frontal lappets are absent.

Frontal lappets are absent in *Limnoscelis* (Romer, 1946), *Diadectes* (Lewis and Vaughn, 1965), anthracosaurs (Panchen, 1970), and *Paleothyris* (Carroll, 1969). Thus, these character-states have the distribution shown in Figure 2B, with the absence of a frontal lappet being the primitive character-state.

Maxilla

In *Dimetrodon, Spenacodon* (Fig. 3F), *Edaphosaurus* (Fig. 3E), and *Ophiacodon* (Fig. 3D), the maxilla does not extend posterior to the orbit and does not meet the quadratojugal. In *Varanops* (Fig. 3C) and *Aerosaurus* (Langston and Reisz, 1981), the maxilla extends posterior to the orbit and meets the quadratojugal, excluding the jugal from the ventral margin of the skull. In cross section, the jugal slopes laterally so that a ridge is present at the contact of the jugal and maxilla. In *Casea* the maxilla meets the quadratojugal, excluding the jugal from the ventral margin of the skull (Fig. 3B). A ridge is present along the contact of the maxilla and jugal as in *Aerosaurus* and *Varanops*.

Thus two structural patterns are present: the *Dimetrodon* pattern in which the jugal enters the ventral margin of the skull and no ridge is present at the contact of the jugal and maxilla, and the *Varanops* pattern in which the jugal is excluded from the ventral margin of the skull by a contact between the maxilla and quadratojugal and a ridge is present along the contact of the maxilla and jugal. *Diadectes* (Fig. 3A), *Limnoscelis (Romer, 1946), Paleothyris* (Carroll, 1969),

---

Figure 4. The skulls in dorsal view of A) *Casea;* B) *Varanops;* C) *Ophiacodon;* D) *Edaphosaurus;* and E) *Sphenacodon.* Reconstruction of *Casea* based on UC 656 and UC 698; *Varanops* based on MCZ 1926 and UR 2423: *Ophiacodon* based on MCZ 1366; *Edaphosaurus* based on MCZ 1762 and USNM 299844; and *Sphenacodon* from Eberth (1981).

Abbreviations: f, frontal; j, jugal; la, lacrymal; na, nasal; op, opisthotic; p, parietal; pf, postfrontal; prf, prefrontal; so, supraoccipital; sq, squamosal; tab, tabular.

and anthracosaurs (Panchen, 1970) are like *Dimetrodon* in these features. Thus, these character-states have the distribution shown in Figure 2B, with the absence of a contact between the maxilla and quadratojugal and the absence of a ridge along the contact of the maxilla and jugal being the primitive character-state.

Quadratojugal

In *Dimetrodon* and *Sphenacodon* (Fig. 3F), the quadratojugal is a small bone sitting on the posterolateral corner of the quadrate and is without an anterior zygomatic process.

Edaphosaurus was reconstructed with a large quadratojugal (Romer and Price, 1940), but specimen MCZ 1762 shows that a small quadratojugal like that of *Dimetrodon* was present (Fig. 3E).

In *Ophiacodon* (Fig. 3D), *Varanops* (Fig. 3C), *Aerosaurus* (Langston and Reisz, 1981), and *Casea* (Fig. 3B), the quadratojugal extends forward from the posterior corner of the skull forming the ventral border of at least the posterior half of the cheek.

In *Diadectes* (Fig. 3A), *Limnoscelis* (Romer, 1946), anthracosaurs (Panchen, 1970), and *Paleothyris* (Carroll, 1969), the quadratojugal is a large element extending well anteriorly. Thus, these character-states have the distribution shown in Figure 2B, with the presence of a large quadratojugal being the primitive condition.

Quadrate Ramus of Pterygoid

In *Dimetrodon* (Fig. 5F), *Sphenacodon,* and *Edaphosaurus* (Fig. 5E), the quadrate ramus of the pterygoid is a vertical sheet with a rounded ventral edge. In *Ophiacodon* (Fig. 5D), *Varanops* (Fig. 5C), and *Casea* (Fig. 5B), a shelf extends medially from the ventral edge of the quadrate ramus, flooring the lateral most part of the tympanic cavity. The quadrate ramus of the pterygoid in *Diadectes* has a similar shelf (Fig. 5A), as does *Limnoscelis* (Romer, 1946). In anthracosaurs, a tympanic shelf is not present, but the quadrate ramus of the pterygoid is little differentiated from the more anterior part of the bone (Panchen, 1970), and is not comparable to the quadrate flange of pelycosaurs in structural details. *Paleothyris* is like *Dimetrodon* and *Edaphosaurus* in not having a medially directed tympanic flange. Thus, these character-states have the distribution shown in Figure 2G, with the presence of a medially

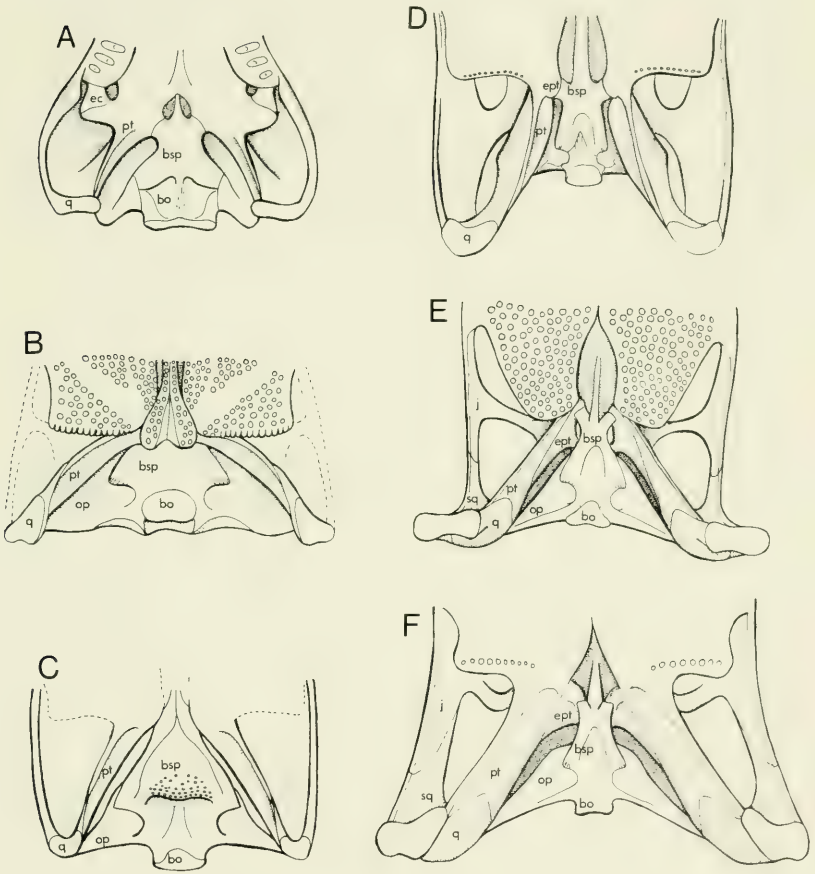


Figure 5. Ventral view of the posterior half of the skulls of A) *Diadectes;* B) *Casea;* C) *Varanops;* D) *Ophiacodon;* E) *Edaphosaurus;* F) *Dimetrodon.* Reconstruction of *Diadectes* based on MCZ 1739 and MCZ 2042; *Casea* based on UC 698; *Varanops* based on P 12841; *Ophiacodon* based on MCZ 1366 and UC 1638; *Edaphosaurus* based on MCZ 1762; and *Dimetrodon* based on MCZ 1365, MCZ 2168, and MCZ 5950.

Abbreviations: bo, basioccipital; bsp, pasisphenoid; ec, ectopterygoid; ept, epipterygoid; j, jugal; op, opisthotic; pt, pterygoid; q, quadrate; sq, squamosal.

directed shelf flooring the tympanic cavity being the primitive character-state and the absence of this flange being a derived condition.

Supraoccipital

In *Dimetrodon, Sphenacodon* (Fig. 6D), *Edaphosaurus* (Fig. 6C), and *Aerosaurus* (Langston and Reisz, 1981), the supraoccipital has an area dorsal to the posttemporal fenestra forming the dorsal margin of the posttemporal fenestra, termed the lateral process by Romer and Price (1940). In *Ophiacodon* (Fig. 6B), the supraoccipital is without an ossified lateral process. Romer and Price interpreted the absence of a lateral process as a result of the tendency for poor ossification in that genus, and reconstructed cartilaginous lateral processes. Reisz (1980) accepted this hypothesis and showed a lateral process of the supraoccipital bordering the posttemporal fenestra in his reconstruction of the occiput of *Ophiacodon.* While cartilaginous lateral processes of the supraoccipital may have been present, these would not have been visible in posterior view since the tabular of *Ophiacodon,* as illustrated by Romer and Price (1940), contacts the opisthotic and has a finished ventral surface that would have formed the dorsal edge of the posttemporal fenstra. In *Casea* (Fig. 6A), the arrangement of the supraoccipital and tabular is like that of *Ophiacodon:* the supraoccipital is not exposed above the posttemporal fenestra when seen in occipital view, and the tabular contacts the paroccipital process, excluding the supraoccipital from the margin of the posttemporal fenestra.

In *Diadectes,* the elements of the occiput are fused. In *Limnoscelis,* the relationships of the tabular are like those of the *Ophiacodon* (Romer, 1946). *Paleothyris* is without lateral processes on the supraoccipital, and the dorsal margin of the posttemporal fenestra is formed by the tabular (Carroll, 1969), as in *Ophiacodon.* However, in contrast to that genus, *Paleothyris* has a large posttemporal fenestra that is bounded medially by the supraoccipital, and thus is not distinctly like either condition seen in pelycosaurs. Thus, these character-states have the distribution shown in Figure 2E, with the exclusion of the supraoccipital from the border of the posttemporal fenestra by the tabular being the primitive character-state, and the presence of a lateral process of the supraoccipital forming the dorsal border of the posttemporal fenestra being a derived character-state.

Basipterygoid Processes

The basipterygoid processes of *Dimetrodon* (Fig. 7G), *Sphenacodon,* and *Edaphosaurus* (Fig. 7F) extend anteriorly, ventrally, and laterally from the lateral surface of the basisphenoid. Each articular surface is divided into two areas, a flat anteroventrally facing area and a dorsally facing area at nearly 90 degrees to this.

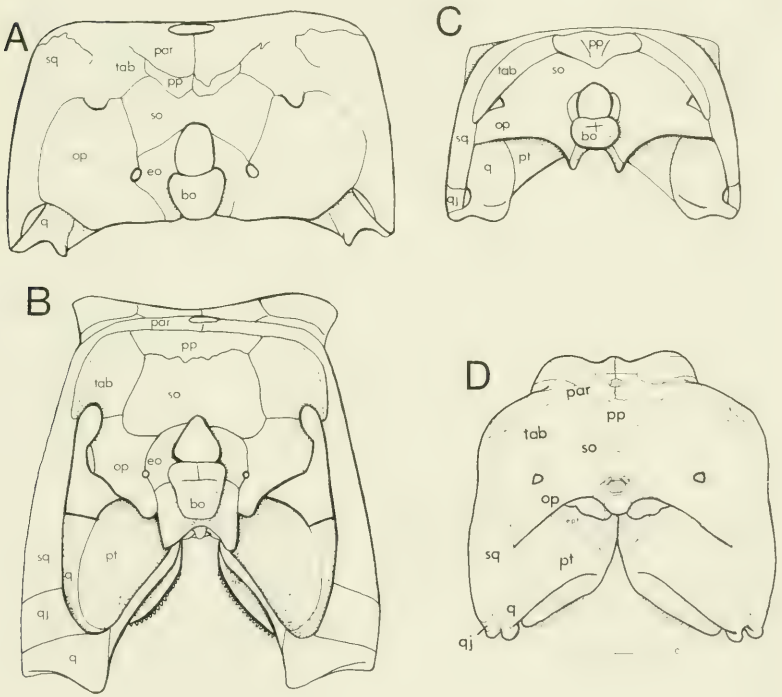


Figure 6. Occipital view of the skulls of A) *Casea;* B) *Ophiacodon;* C) *Edaphosaurus;* and D) *Sphenacodon.* Drawing of *Casea* based on UC 698 and UC 656; *Ophiacodon* based on MCZ 1366, MCZ 1426, and MCZ 1121; *Edaphosaurus* based on MCZ 1762; and *Sphenacodon* from Eberth (1981).

Abbreviations: bo, basioccipital; eo, exoccipital; op, opisthotic; par, parietal; pp, postparietal; q, quadrate; qj, quadratojugal; sq, squamosal; tab, tabular.

In *Ophiacodon,* the basipterygoid processes extend ventrally (Fig. 7E). The long axis of the articular surfaces are anteroposteriorly oriented and the surface curves smoothly from its ventral to its lateral aspect.

In *Casea* (Fig. 7C), the basipterygoid processes extend laterally from the side of the cultriform process and have strongly curved articular surfaces. *Aerosaurus* (Langston and Reisz, 1981) is similar to *Casea,* but differs in that the articular surfaces are more elongate mediolaterally.

Thus, two distinct characters can be recognized in the structure of the basipterygoid process. One of these is the curvature of the articular surfaces: the curved articular surfaces such as are seen in *Aerosaurus* being one character-state and two flat articular surfaces set at

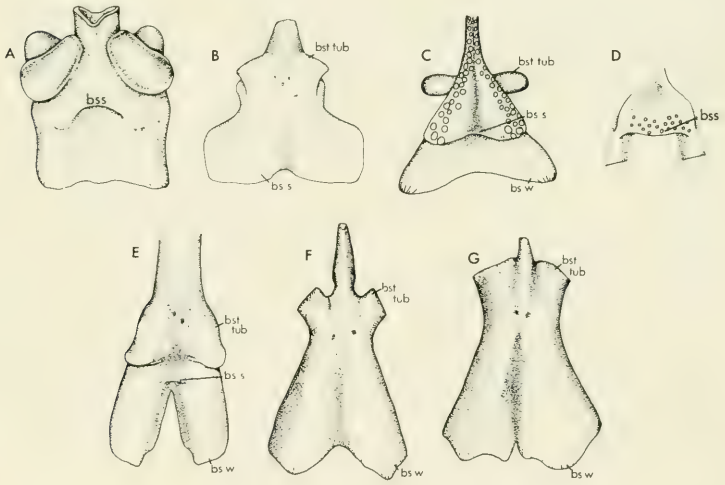


Figure 7. The basisphenoid in ventral view of A) *Archeria,* B) *Diadectes,* C) *Casea,* D) *Varanops,* E) *Ophiacodon,* F) *Edaphosaurus,* and G) *Dimetrodon.* Drawing of *Archeria* based on MCZ 8736; *Diadectes* based on MCZ 3277; *Casea* based on UC 698; *Varanops* based on UR 2423; *Ophiacodon* based on UC 1638 and MCZ 4820; *Edaphosaurus* based on MCZ 1762; and *Dimetrodon* based on MCZ 1697.

Abbreviations: bs s, basisphenoid shelf; bs w, basisphenoid wings; bst tub, basipterygoid tubercula.

nearly 90 degrees to each other such as in *Dimetrodon* being a second character-state. In *Diadectes* (Fig. 7B), *Archeria* (Fig. 7A), and *Eocaptorhinus* (Heaton, 1979), the basipterygoid processes are curved. Thus, for the character of the curvature of the articular surfaces, the character-states have the distribution shown in Figure 2B, with the presence of curved articular surfaces being the primitive character-state and the flat articular surfaces of *Dimetrodon, Sphenacodon,* and *Edaphosaurus* being a derived character-state.

The second character is the orientation of the basipterygoid processes: the laterally oriented basipterygoid processes such as is seen in *Aerosaurus* being one character-state, anteroventrally oriented processes such as is seen in *Dimetrodon* being a second character-state, and ventrally oriented basipterygoid processes with anteroposteriorly oriented articular surfaces such as is seen in *Ophiacodon* being a third character-state. In all the outgroups, the basipterygoid processes extend ventrolaterally from the side of the cultriform process as in *Dimetrodon.* Thus, for the character of the orientation of the basipterygoid processes, the character-states have the distribution shown in Figure 2B, with the presence of ventrolaterally oriented basipterygoid processes being the primitive character-state. The laterally orientated basipterygoid process seen in *Casea* and *Aerosaurus* is one derived character-state, and the ventrally oriented basipterygoid process with anteroposteriorly oriented articular surfaces of *Ophiacodon* is a second derived character-state.

Shelf Between Basisphenoid Wings

In *Dimetrodon* (Fig. 7G), *Sphenacodon,* and *Edaphosaurus,* the basisphenoid wings extend posteriolaterally from the base of the basipterygoid tubercula with a smooth trough between them. In *Ophiacodon,* the arrangement of the basisphenoid wings is similar, but a shelf (bs.s., Fig. 7E) extends between the base of the wings, roofing over the anterior end of the trough. This is also the case in *Varanops* (Fig. 7D) and *Aerosaurus* (Langston and Reisz, 1981). In *Casea* (Fig. 7C), a basisphenoid shelf is present, although its posterior edge, rather than being straight, is V-shaped with the lateral ends of the V raised.

In *Limnoscelis* (Romer, 1946), a shelf is present roofing the anterior portion of the trough between the basisphenoid wings. In *Diadectes,* this shelf is hypertrophied and extends to the posterior ends

of the basisphenoid wings so that, in ventral view, the shelf appears to occupy the position of the wings (Fig. 7B). The anthracosaur *Archeria* is like *Limnoscelis* in having a shelf covering the anterior portion of the trough between the basisphenoid wings (Fig. 7A). *Paleothyris* is without such a shelf.

Thus, these character-states have the distribution shown in Figure 2F, with the presence of a shelf between the bases of the basisphenoid wings being the primitive character-state, and the absence of the shelf being a derived condition.

Stapes

The stapes of *Dimetrodon* (Fig. 8E) consists of a triangular plate oriented anteromedially with a posteromedially oriented footplate (fp., Fig. 8E) directed about 90 degrees from the medial edge of the triangular plate. The wide end of the triangle is the dorsal process (dp., Fig. 8E), and the narrow end is the quadrate process (qp., Fig. 8E). The dorsal process articulates in a socket on the ventral surface of the paroccipital process.

The stapes of *Edaphosaurus* (Fig. 8C) differs from that of *Dimetrodon* only in proportions, the dorsal process being relatively wider

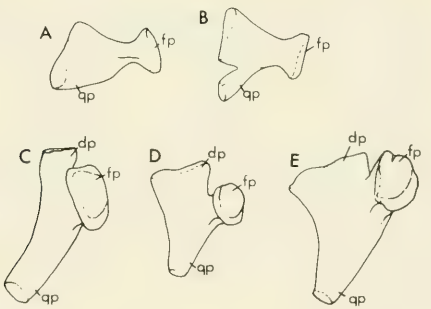


Figure 8. The left stapes in posterior view of A) *Casea;* B) *Varanops;* C) *Ophiacodon;* D) *Edaphosaurus;* E) *Dimetrodon.* Drawing of *Casea* based on UC 698; *Varanops* based on UR 2423; *Ophiacodon* based on MCZ 1366; *Edaphosaurus* based on MCZ 1762; and *Dimetrodon* based on MCZ 1347.

Abbreviations: dp, dorsal process; fp, footplate; qp, quadrate process.

and the quadrate process shorter. The dorsal process articulates in a socket on the paroccipital process as in *Dimetrodon.*

In *Ophiacodon* (Fig. 8C), the stapes is more rodlike than *Dimetrodon.* The dorsal process of the stapes is narrower, although it still articulates in a socket on the paroccipital process, and the footplate is oval, rather than circular in end view as in *Dimetrodon* and *Edaphosaurus.*

In *Casea* (Fig. 8A), the stapes consists of a footplate and a single triangular flange of bone extending laterally from this. One corner of the flange approaches the paroccipital process and presumably represents the base of the unossified dorsal process. The other corner is directed towards the stapedial pit of the quadrate. A distinct socket in the paroccipital process for the dorsal process of the stapes is not present.

The stapes of *Varanops* (Fig. 8B) differs from that of *Casea* in the presence of a V-shaped notch in its lateral edge. The edges of this notch are damaged, and therefore the notch may be articicial. In other regards, the stapes is directly comparable to that of *Casea.* As in *Casea,* no socket is present on the paroccipital process for the dorsal process of the stapes.

The stapes of *Aerosaurus* is not known, but the paroccipital process shows no articular surface for the dorsal process of the stapes (Langston and Reisz, 1981).

The stapes of *Paleothyris* (Carroll, 1969) appears most similar to the rodlike laterally directed stapes in captorhinids (Heaton, 1979), in which the dorsal process does not articulate in a socket on the paroccipital process. The stapes of *Diadectes,* as described by Olson (1966) is not readily comparable to that of any other tetrapod. A stapes is not known in *Limnoscelis* or anthracosaurs. In the early temnospondyle *Greererpeton,* the stapes is similar to that of *Varanops* and *Casea* in the presence of a triangular lateral process that does not have an ossified dorsal head articulating in a socket on the paroccipital process (Carroll, 1980). Since *Greererpeton* and pelycosaurs are both without an otic notch, probably primitively so (Lombard and Bolt, 1979; Carroll, 1980), the similarity of the stapes in these animals can be used as evidence that the stapes of *Casea* and *Varanops* is primitive in not having a socket on the paroccipital process that receives the dorsal process of the stapes.

Prearticular

In *Dimetrodon* (Fig. 9C), *Sphenacodon,* and *Edaphosaurus,* the prearticular underlies the pterygoideus process of the articular, a distinctive twisting of the bone being present as it passes under the process.

In *Ophiacodon* (Fig. 9A), the prearticular underlies the medial portion of the articular but does not show the twisting seen in *Dimetrodon.* This is also the case in *Varanops* (Fig. 10) and *Aerosaurus* (Langston and Reisz, 1981). The condition in *Casea* is unknown.

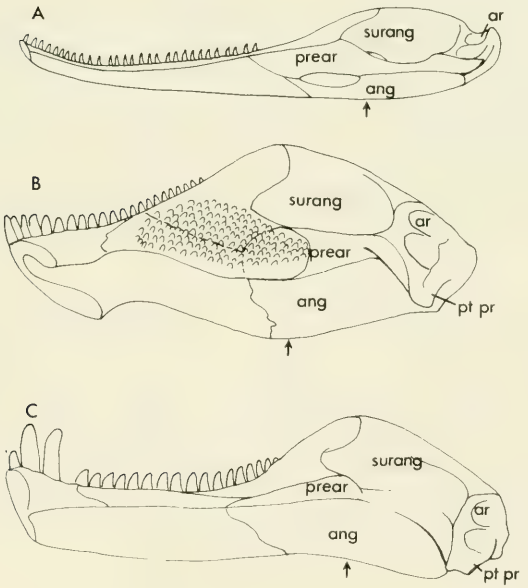


Figure 9. The right lower jaw in medial view of A) *Ophiacodon;* B) *Edaphosaurus;* C) *Dimetrodon.* From Romer and Price, 1940.

Abbreviations: ang, angular; ar, articular; prear, prearticular; pt pr, pterygoideus process; sur ang, surangular. Arrows indicate the position of sections shown in Figure 11.

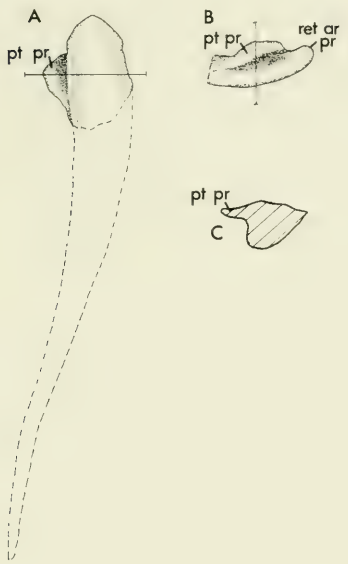


Figure 10. The lower jaw of *Varanops* in A) ventral view; B) medial view of articular region; and C) section through articular and pterygoideus process. Drawings based on MCZ 1926.

Abbreviations: pt pr, pterygoideus process; ret ar pr, retroarticular process.

Didaectes is without the twisting of the prearticular, as are captorhinids (Heaton, 1979), and anthracosaurs (Panchen, 1970). Thus, these character-states have the distribution shown in Figure 2B, with the absence of a twisted prearticular being the primitive character-state.

Angular

In *Dimetrodon* (Fig. 11E) and *Sphenacodon* the angular is a vertically oriented plate that supports the prearticular and surangular by its dorsal edge (Fig. 11E), and the articular by its medial surface. The posterior edge of the angular is notched, forming the reflected lamina of the angular.

The angular of *Edaphosaurus* (Fig. 11D) and *Ophiacodon* (Fig. 11C) is like that of *Dimetrodon* in being a vertically oriented plate. They differ in that they are without a posterior notch.

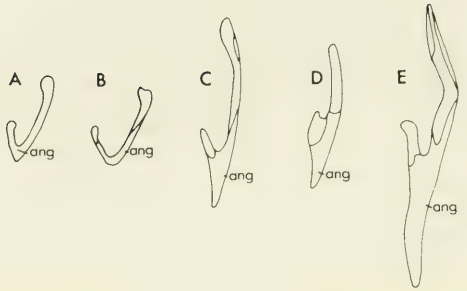


Figure 11. Sections through the postdentary bones of the lower jaw at the position just posterior to the dentary (marked by an arrow for the jaws shown in Figure 9). A) *Varanops;* B) *Casea;* C) *Ophiacodon;* D) *Edaphosaurus;* and E) *Dimetrodon.* Drawing of *Varanops* based on UR 2423; *Casea* based on UC 698; *Ophiacodon, Dimetrodon* and *Edaphosaurus* from Romer and Price, 1940.

Abbreviation: ang, angular.

In *Casea* (Fig. 11A), *Varanops* (Fig. 11B), and *Aerosaurus* (Langston and Reisz, 1981), the angular is a troughlike bone. In *Varanops,* a keel is present on its ventral edge, but in no position along the angular does the bone form an extended vertical plate.

The angular in *Limnoscelis* and *Diadectes* is like that of *Casea* and *Varanops* in being troughlike. In *Paleothyris,* a keel is present in the region of the angular, but the bone does not form an extended vertical plate. Thus, these character-states have the distribution shown in Figure 2B, with the absence of an extended vertical plate being the primitive character-state.

Pterygoideus Process of Articular

In *Dimetrodon* (Fig. 9C), *Sphenacodon,* and *Edaphosaurus* (Fig. 9C), a pterygoideus process is present as a distinct process on the articular. In primitive species of *Dimetrodon,* and in *Sphenacodon* and *Edaphosaurus,* this is located medial to the glenoid.

In *Ophiacodon* (Fig. 9A) a distinct pterygoideus process is not present on the articular. A flange on the prearticular just anterior to the articular may be functionally equivalent to the pterygoideus process of *Dimetrodon.*

In *Varanops* (Fig. 10) and *Aerosaurus* (Langston and Reisz, 1981), a pterygoideus process is not present on the articular,

although a well-developed flange on the prearticular just anterior to the articular is present. The condition in *Casea* is unknown.

In *Diadectes,* the articular does not have a distinct pterygoideus process. The articular extends medially from the inner surface of the jaw (Romer, 1956; Fig. 107C), but the medially projecting portion is located beneath the medial condyle of the gleniod and is not a distinct process. No flange is present on the prearticular anterior to the articular. This is also the case in anthracosaurs (Panchen, 1970). The internal surface of the articular is not known in *Paleothyris.* In captorhinids, a pterygoideus process is absent or poorly developed, although a medial flange formed by the prearticular just anterior to the articular is present (Heaton, 1979). Thus, these character-states have the distribution shown in Figure 2D, with the absence of a pterygoideus process being primitive for tetrapods, the presence of a flange on the prearticular just anterior to the articular being primitive for reptiles, and the presence of a pterygoideus process formed by the articular being a derived feature within pelycosaurs.

Neural Arch

In *Dimetrodon* (Fig. 12F) and *Sphenacodon,* the neural arch has a pit in its lateral surface above the level of the transverse process. In *Edaphosaurus boanerges* (Fig. 12E), the neural arch is without pits, although in an undescribed species of *Edaphosaurus* from near Garnett, Kansas, *Sphenacodon*-like pits are present along the length of the column (Reisz *et al.,* 1982). *Varanops* (Fig. 12C) and *Aerosaurus* (Langston and Reisz, 1981) are like *Dimetrodon* in having a pit in the lateral surface of the neural arch. *Ophiacodon* (Fig. 12D) and *Casea* (Fig. 12B) are without a pit in the lateral surface of the neural arch.

The neural arches of *Limnoscelis, Diadectes,* anthracosaurs, and *Paleothyris* are without pits. Thus, these character-states have the distribution shown in Figure 2B, with the absence of pits in the neural arch being the primitive character-state.

Transverse Processes

In *Dimetrodon* (Fig. 12F) and *Sphenacodon,* the longest transverse processes are in the area of the posterior cervicals and anterior dorsals. They extend laterally a distance about equal to the width of the centrum.

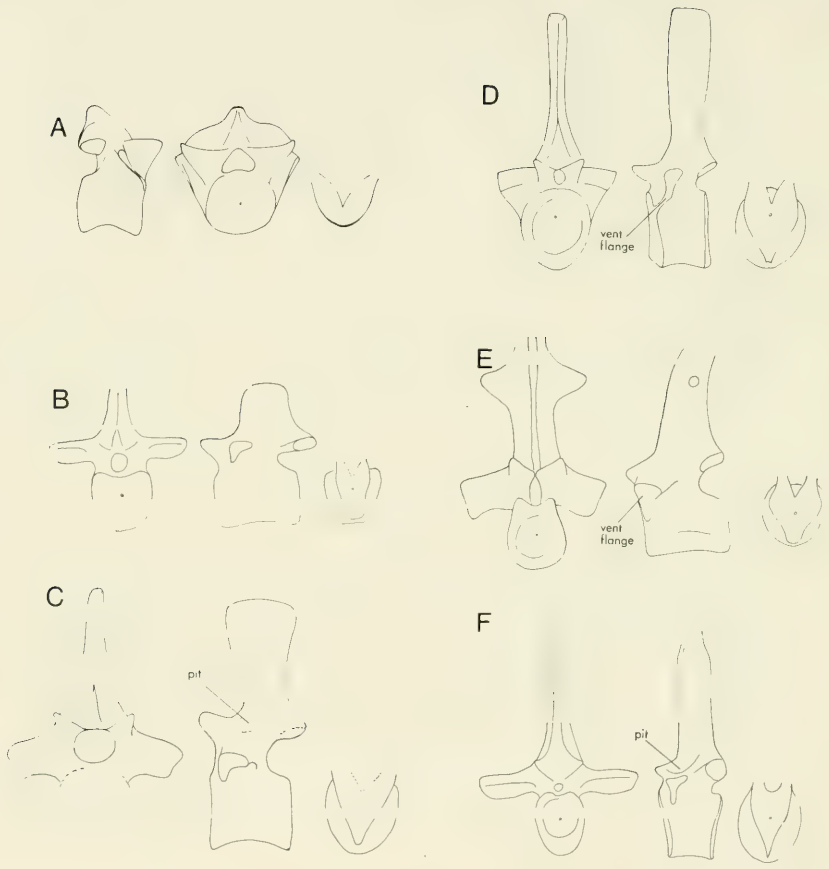


Figure 12. Anterior dorsal vertebrae in lateral and anterior view, and a cross section of an anterior dorsal centrum of A) *Labidosaurus;* B) *Casea;* C) *Varanops;* D) *Ophiacodon;* E) *Edaphosaurus;* and F) *Dimetrodon.* Drawing of *Labidosaurus* based on MCZ 8724; *Casea* based on P 12841; *Varanops* based on MCZ 1926; *Ophiacodon* based on MCA 5912; *Edaphosaurus* based on MCZ 1359; and *Dimetrodon* based on MCZ 5216.

Abbreviations: pit, pit in the lateral surface of the neural arch; vent flange, ventral flange supporting the transverse process.

In *Edaphosaurus,* the longest transverse processes are shorter than the width of the centrum and the transverse processes are braced by a vertical flange of bone ventrally.

Ophiacodon (Fig. 12D) has short transverse processes directed more ventrally than in *Edaphosaurus* and *Dimetrodon.* The ventral flange forms a complete web of bone connecting the transverse proces to the anterior edge of the centrum.

Varanops (Fig. 12C), *Aerosaurus* (Langston and Reisz, 1981), and *Casea* (Fig. 12B) have long laterally directed transverse processes. *Limnoscelis, Diadectes,* anthracosaurs, and *Paleothyris* all have short transverse processes, although only in captorhinids (Fig. 12A) are these supported by a web of bone that extends to the anterior edge of the centrum. Thus, for the character of the transverse processes, the character-states have the distribution shown in Figure 2D, with the presence of short transverse processes connected to the anterior edge of the centrum by a web of bone being the primitive character-state for reptiles, and the long transverse processes being a derived character-state present within pelycosaurs.

Centrum

In *Dimetrodon* (Fig. 12F) and *Sphenacodon,* the vertebrae in the cervical and anterior to mid-dorsal regions of the vertebral column have well-developed keels.

In *Edaphosaurus* (Fig. 12E), keels are present only on the cervical vertebrae. The dorsal vertebrae have broadly rounded ventral surfaces.

In *Ophiacodon* (Fig. 12D), the cervical vertebrae are keeled. The mid-dorsal vertebrae are wedge-shaped in cross section but have a pair of ridges ventrally, rather than a single keel. The posterior dorsal and lumbar vertebrae are circular in end view.

In *Varanops* (Fig. 12C), the cervical and mid-dorsal vertebrae are keeled.

In *Casea* the most anterior cervical vertebrae are unknown. All the more posterior vertebrae are without keels (Fig. 12B). In cross section, the centra have flatter ventral surfaces than in *Edaphosaurus.*

The centra of *Diadectes* and *Limnoscelis* are not specifically similar to any pelycosaur. In cross section, they are generally wedge-shaped, but are without a distinct keel. The vertebrae of *Protero-*

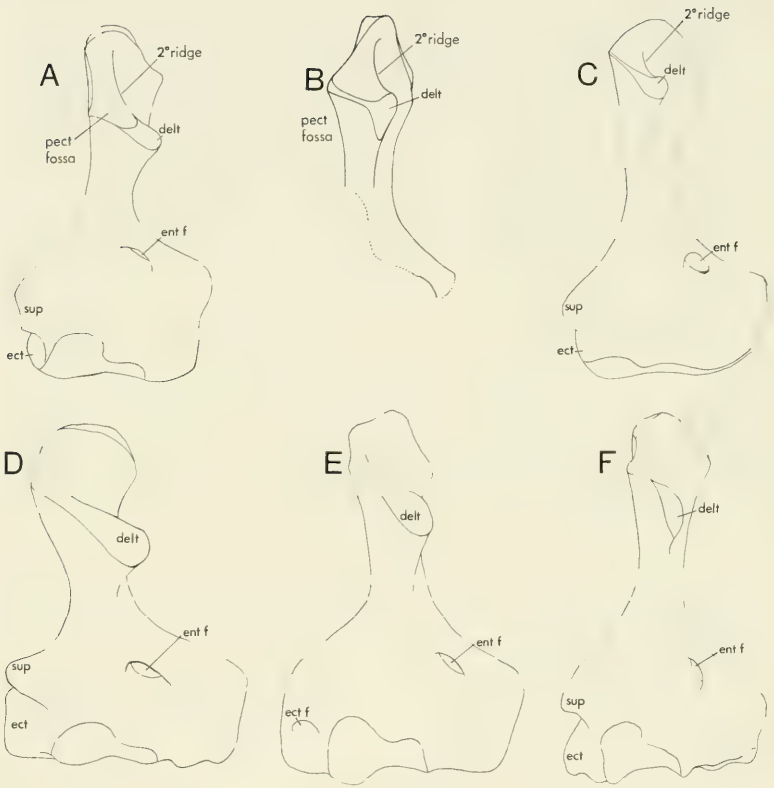


Figure 13. The humerus in distal ventral view of A) *Casea;* B) *Aerosaurus;* C) *Varanops;* D) *Ophiacodon;* E) *Edaphosaurus;* and F) *Dimetrodon.* Drawing of *Casea* from Williston (1911), drawing of *Aerosaurus* based on UC 464; *Varanops* based on UR 695; *Ophiacodon* based on MCZ 1486; *Edaphosaurus* based on MCZ 3417; *Dimetrodon* based on MCZ 1304.

Abbreviations: delt, deltopectoral crest; ect, ectepicondyle; ect f, ectepicondylar foramen; ent f, entepicondylar foramen; pect fossa, pectoralis fossa; sup, supinator process; 2° ridge, secondary pectoralis ridge.

gyrinus an anthracosaur with a protoreptilian vertebral pattern (Holmes and Carroll, 1977), are without keels. This is also the case in captorhinids (Fig. 12A). Thus, the absence of a distinct keel can be considered a primitive feature.

Deltopectoral Crest

In *Sphenacodon* and *Dimetrodon* (Fig. 13F), the deltopectoral crest has a bulbous distal end and a sharp knife-edge base. In *Ophiacodon* and *Edaphosaurus,* the distal end of the deltopectoral crest is bulbous, but the proximal end is a broad ridge (Fig. 13 D–E).

In *Varanops* (Fig. 13C), *Aerosaurus* (Fig. 13B), and *Casea* (Fig. 13A), a secondary ridge is present extending from the distal end of the deltopectoral crest to a more medial position on the proximal end of the humerus. In *Casea* and *Aerosaurus,* this is a sharp crest that results in the presence of a distinct fossa at the base of the deltopectoral crest. In *Varanops* this is a low, rounded ridge.

In captorhinids (Holmes, 1977), the crest is absent. The tuberosity is located on the lateral edge of the proximal end of the humerus. In *Diadectes,* the deltopectoral crest is like that of *Ophiacodon,* although it forms a more obtuse angle with the proximal end of the humerus. Thus, these character-states have the distribution shown in Figure 2E, with the presence of a deltopectoral crest formed by a single broad ridge extending from the tuberosity to the proximal end of the bone being a primitive reptilian condition, and the presence of a secondary ridge extending from the deltopectoral tuberosity to the proximal end of the bone being a derived condition.

Results

The distribution of the character-states for which polarity can be interpreted, and the cladogram that requires the fewest number of reverseals or convergent evolutionary events to explain this distribution, is shown in Figure 14.

CHARACTER ANALYSIS: II. FEATURES FOR WHICH POLARITY CANNOT BE INTERPRETED

As argued in the materials and methods section, characters for which polarity of the character-states cannot be interpreted are of use in providing a test of the caldogram presented on the basis of other characters. Three such characters are considered here.

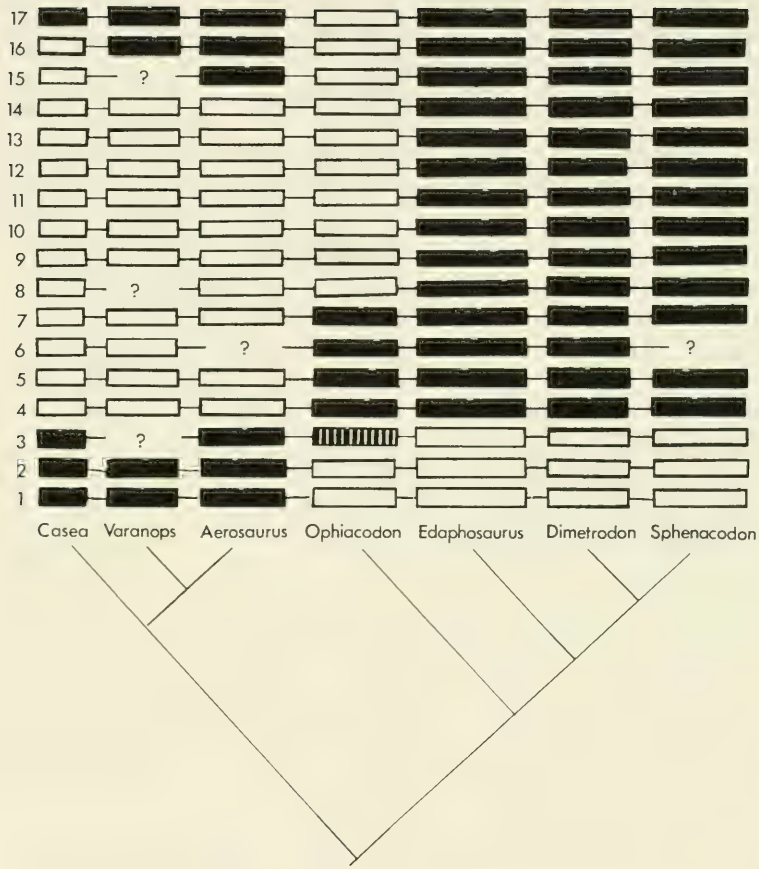


Figure 14. Hypothesis of relationships of selected genera of pelycosaurs based on the characters described in the text for which polarity can be interpreted. □ indicate primitive character-states, ■ and ▥ indicate derived character-states. For description of characters and character-states see Table 2.

Table 2. The characters that form the basis for the cladogram shown in Figure 14. The numbers refer to the characters shown in Figure 14.

1) humerus, deltopectoral crest:
primitive character-state: the presence of a single ridge leading from the distal end of the deltopectoral crest to the proximal end of the humerus;
derived character-state: the presence of a secondary ridge leading from the distal end of the deltopectoral crest to a more medial position on the proximal end of the humerus with a fossa at the base of the crest.

2) maxilla:
primitive character-state: no contact between the maxilla and the quadratojugal;
derived character-state: the maxilla contacts the quadratojugal with the bones raised to form a ridge along the contact of the maxilla and jugal.

3) basipterygoid process:
primitive character-state: basipterygoid process directed anteroventrally;
derived character-state #1 (indicated by ■ in Figure 14): basipterygoid process directed laterally and are mediolaterally elongate;
derived character-state #2 (indicated by ▥ in Figure 14): basipterygoid processes directed ventrally and articular surface oriented anteroposteriorly.

4) cheek margin:
primitive character-state: cheek margin convex;
derived character-state: cheek margin concave.

5) premaxilla:
primitive character-state: anterior margin of the premaxilla extends anteriorly from the anterior termination of the tooth row;
derived character-state: anterior margin of the premaxilla slopes posteriorly from the anterior termination of the tooth row.

6) stapes:
primitive character-state: dorsal process of stapes not articulating in socket on the paroccipital process;
derived character-state: dorsal process of stapes articulating in a socket on the paroccipital process.

7) angular:
primitive character-state: angular without an extended ventral plate in the region anterior to the articular;
derived character-state: angular with an extended ventral plate in the region of the articular.

8) basipterygoid articular surfaces:
primitive character-state: articular surfaces curved;
derived character-state: articular surfaces differentiated into two flat areas at right angles to each other.

9) shelf between basisphenoid wings:
primitive character-state: shelf between basisphenoid wings present;
derived character-state: no shelf between basisphenoid wings.

Table 2. Continued

10) frontal:
primitive character-state: frontal without a lateral lappet;
derived character-state: frontal with a lateral lappet.

11) quadratojugal:
primitive character-state: quadratojugal extends anteriorly forming ventral margin of skull along posterior half of cheek;
derived character-state: quadratojugal restricted to ventro-lateral corner of skull.

12) prearticular;
primitive character-state: prearticular not twisted;
derived character-state: prearticular twisted.

13) pterygoideus process:
primitive character-state: pterygoideus process not formed by articular alone;
derived character-state: pterygoideus process formed entirely by articular.

14) quadrate ramus of pterygoid:
primitive character-state: quadrate ramus of pterygoid with a medially directed tympanic flange along its ventral edge;
derived character-state; quadrate ramus of pterigoid with rounded ventral edge.

15) supraoccipital:
primitive character-state: supraoccipital without a lateral process, dorsal border of posttemporal fenestra formed by tabular;
derived character-state: supraoccipital with a lateral process that forms the dorsal border of the posttemporal fenestra.

16) neural arch:
primitive character-state: neural arch without pits;
derived character-state: neural arch with pits on its lateral surface at the level of the zygapophyses.

17) transverse processes:
primitive character-state: transverse processes supported by a web of bone extending to the anterior edge of the centrum;
derived character-state: transverse processes extend laterally, ventral flange not extending to the anterior edge of the centrum.

Postparietal

In *Dimetrodon, Sphenacodon* (Fig. 6D), and *Edaphosaurus* (Fig. 6C), the postparietal is a single median element that broadly overlies the supraoccipital.

The *Ophiacodon,* a postparietal was not observed, but the supraoccipital shows that the postparietal did not greatly overlap that bone.

In *Casea* (Fig. 6A), the postparietal is a paired element.

The postparietal of *Varanops* and *Aerosaurus* is unknown.

Limnoscelis is like *Dimetrodon* and *Edaphosaurus* in having a single postparietal (Romer, 1946). In anthracosaurs, as in primitive tetrapods generally, the postparietal is a paired element (Panchen, 1970).

Two explanations for this distribution of character-states are equally possible: that *Limnoscelis* is apomorphic in having a single postparietal and a paired postparietal is primitive for reptiles, or that a single postparietal is primitive for reptiles and *Casea* is derived in having a paired postparietal. In view of this, the presence of single or paired postparietals must be considered character-states for which polarity cannot be determined.

Paroccipital processes

The paroccipital processes in *Dimetrodon* and *Sphenacodon* are rodlike structures sloping ventrally and posteriorly. In cross section, they are triangular with their height less than twice their width. In *Edaphosaurus,* the processes are like those in *Dimetrodon,* but they are shorter and extend more directly laterally (Fig. 6C). In *Ophiacodon,* the process is short and laterally directed (Fig. 6B). It is rodlike, although its distal end is unossfied so that, as preserved, it does not reach the cheek. In *Varanops* (Fig. 4B) and *Aerosaurus* (Langston and Reisz, 1981), the paroccipital process is platelike: in lateral view its height is more than three times its width. In *Casea,* the platelike nature of the paroccipital process is exaggerated (Fig. 6A).

Thus, two distinct character-states can be recognized: one present in *Varanops* and *Casea* in which the paroccipital process is platelike, and one seen in *Ophiacodon, Edaphosaurus, Dimetrodon,* and *Sphenacodon* in which the paroccipital process is rodlike. The paroccipital process of *Limnoscelis,* as described by Romer (1946), is not directly comparable to either pelycosaur condition. The paroccipital process of *Paleothyris* is unossified (Carroll, 1969). Thus, there is no basis for interpreting the polarity of these character-states.

Supinator Process

In *Dimetrodon* and *Sphenacodon,* the supinator process is elongate proximodistally, and its distal end curves distally (Fig. 13F).

In *Edaphosaurus* (Fig. 13E), an ectepicondylar foramen is present. Romer and Price (1940) interpreted this as a result of the development of a bony connection between the ectepicondyle and the distal end of the supinator process. Without this connection, the supinator process would have the morphology of that of *Dimetrodon.*

In *Ophiacodon* (Fig. 13D), the supinator process is a narrow triangular process that projects laterally.

Casea (Fig. 13A) and *Varanops* (Fig. 13C) are like *Dimetrodon* in the development of their supinator process. The morphology of the process in an adult humerus of *Aerosaurus* is not known.

The structure of the supinator process is variable in early tetrapods. In anthracosaurs, this is represented by a crest running the full length of the humerus (Panchen, 1970). In *Limnoscelis* and *Diadectes,* it is a narrow laterally directed process located distal to the radial condyle (Romer, 1956). In its shape, it is like that of *Ophiacodon,* but in *Ophiacodon,* as in other pelycosaurs and in contrast to *Diadectes* and *Limnoscelis,* the supinator process is located distally and is separated from the radial condyle by a distinct groove. The supinator process of *Paleothyris* is located near the distal end of the humerus and is separated from the radial condyle by a groove (Carroll, 1969). Its shape does not compare directly with either pelycosaur condition. This distribution of character-states does not allow polarity of the character in pelycosaurs to be interpreted.

Results

The characters for which polarity cannot be interpreted can be separated into two groups: those whose distribution does not require hypothesizing the occurrence of parallel evolution, and those whose distribution requires a more complicated hypothesis of evolution of the character. In the first group are the structure of the paroccipital process and the presence of paired postparietals. The structure of the paroccipital process is in accordance with the separation of *Ophiacodon, Edaphosaurus, Dimetrodon,* and *Sphenacodon* from *Aerosaurus, Varanops,* and *Casea,* and thus is in agreement with the separation of pelycosaurs into these two groups.

In the second group is the structure of the supinator process. If the supinator process of *Ophiacodon* is autapomorphic, these character-states are consistent with the cladogram; if primitive, then

the proximodistally elongate supinator process must have evolved independently in the clade including *Casea* and *Varanops* and the clade including *Edaphosaurus, Dimetrodon,* and *Sphenacodon.* Thus, this character is not necessarily in conflict with the cladogram, but requires a more restrictive hypothesis of polarities to account for the distribution of the character-states.

DISCUSSION

These results differ from those of Reisz (1980) in three features: 1) *Edaphosaurus* and *Dimetrodon* are interpreted as members of a clade more derived than *Ophiacodon;* 2) *Varanops* and *Aerosaurus* are interpreted as being more primitive than the clade including *Ophiacodon, Edaphosaurus, Dimetrodon,* and *Sphenacodon;* and 3) *Casea, Varanops,* and *Aerosaurus* are interpreted as being members of a single clade distinct from the clade including *Ophiacodon, Edaphosaurus,* and *Dimetrodon.*

The more primitive position of *Ophiacodon* relative to *Edaphosaurus* and *Dimetrodon* is the same as that in the phylogeny proposed by Romer and Price (1940). The alternate interpretation of relationships of these genera proposed by Reisz (1980) was based primarily on cranial features, including the structure of the frontal, supratemporal, and the proportions of the skull. The structure of the frontal of *Edaphosaurus* was incorrectly interpreted by Romer and Price (1940). As discussed above, the frontal of *Edaphosaurus* is directly comparable to that of *Dimetrodon,* and the frontals in these animals share features that can be interpreted as being derived with respect to *Ophiacodon.* Thus, the frontal supports a relationship between *Edaphosaurus* and *Dimetrodon,* rather than between *Ophiacodon* and *Dimetrodon.* The structure of the supratemporal is poorly known in most genera. The element that Romer and Price identified as the supratemporal in *Casea* is better interpreted as the proximal end of the squamosal. This is also the case in *Edaphosaurus.* Thus, this character cannot be used at present in interpreting pelycosaur interrelationships. The proportions of the skull of *Edaphosaurus* are not known with sufficient certainty to be used in interpreting relationships.

The position of *Varanops* and *Aerosaurus* is the most striking difference from both the cladogram of Reisz (1980) and the phylogeny of Romer and Price (1940). This difference is based on the

interpretation that *Ophiacodon* and *Dimetrodon* share derived cranial features not present in *Varanops* and *Aerosaurus*, and that *Casea*, *Varanops*, and *Aerosaurus* share derived cranial features not present in *Ophiacodon*. Necessarily, we interpret the derived vertebral features shared in *Dimetrodon* and *Varanops*, the features that Romer and Price used to unite these genera, as convergent.

The suggestion that *Casea*, *Varanops*, and *Aerosaurus* are members of a single clade is the least well supported of the relationships proposed above. This reflects the problems inherent in determining relationships of primitive members of clades. Greater certainty about the primitive character-state of various features in pelycosaurs will come from a better understanding of the interrelationships of early reptiles and the use of an out-group that is more closely related to pelycosaurs than are diadectomorphs in the analysis of polarities. This will allow better separation of characters that are primitive for pelycosaurs from those that are derived for the clade including *Casea* and *Varanops*.

ACKNOWLEDGMENTS

The authors are greatly indebted to the scientific and curatorial staff of the Field Museum of Natural History and the American Museum of Natural History for permission to study specimens in their collections. Grants from the K. P. Schmitt Fund of the Field Museum enabled the authors to visit the Field Museum. Versions of this manuscript were read by J. Hopson, H. Barghusen, R. Reisz, M. Heaton, F. Jenkins, Jr., H. Sues, and G. Meyer. Their critical comments substantially improved the manuscript.

Publication costs of this study were covered in part by a grant from the Wetmore Colles Fund.

LITERATURE CITED

Carroll, R. L. 1964. The earliest reptiles. J. Linn. Soc. (Zool.), **45**: 61–83.

———. 1969. A Middle Pennsylvanian captorhinomorph and the interrelationships of primitive reptiles. J. Paleontol., **43**: 151–170.

———. 1970. The ancestry of reptiles. Phil. Trans. Roy. Soc. Lond. B, **257**: 267–308.

———. 1980. The hyomandibular as a supporting element in the skull of primitive tetrapods pp. 293–317. *In* A. L. Panchen (ed.), The Terrestrial

Environment and the Origin of Land Vertebrates, London and New York, Academic Press.

EBERTH, D. 1981. The skull of *Sphenacodon ferocior* and comparisons within the subfamily Sphenacodontinae. MSc thesis, Department of Paleontology, Berkeley, University of California.

HEATON, M. H. 1979. Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian, Oklahoma and Texas. Oklahoma Geol. Surv. Bull. No. 127, 84 pp.

———. 1980. The Cotylosauria: A reconsideration of a group of archaic tetrapods, pp. 479–551. *In* A. L. Panchen (ed.), The Terrestrial Environment and the Origin of Land Vertebrates, London and New York, Academic Press.

HOLMES, R. 1977. The osteology and musculature of the pectoral limb of small captorhinids. J. Morphol., **152**: 101–140.

HOLMES, R., AND R. L. CARROLL. 1977. A temnospondyl amphibian from the Mississippian of Scotland. Bull. Mus. Comp. Zool., **147**: 489–511.

KEMP, T. S. 1980. Origin of mammal-like reptiles. Nature, **283**: 378–380.

LANGSTON, W. 1965. *Oedaleops campi* (Reptilia: Pelycosauria). A new genus and species from the Lower Permian of New Mexico and the family Eothyrididae. Bull. Texas Mem. Mus., **9**: 1–46.

LANGSTON, W., AND R. REISZ. 1981. *Aerosaurus wellesi,* new species, a varanopseid mammal-like reptile (Synapsida: Pelycosauria) from the Lower Permian of New Mexico. J. Vertebr. Paleontol., **1**: 73–96.

LEWIS, G. E., AND P. P. VAUGHAN. 1965. Early Permian vertebrates from the Cutler Formation of the Placerville area, Colorado. Contrib. Paleontol. Geol. Surv. Prof. Pap. No. 503-C, pp. 1–46.

LOMBARD, R. E., AND J. R. BOLT. 1979. Evolution of the tetrapod ear: an analysis and reinterpretation. Biol. J. Linn. Soc., **11**: 19–76.

OLSON, E. C. 1966. The middle ear—morphological types in amphibians and reptiles. Am. Zool., **6**: 399–419.

PANCHEN, A. L. 1970. Batrachosauria, part A, Anthracosauria. *In* O. Kuhn (ed.), Handbuch der Palaoherpetologie, Stuttgart, Germany and Portland, USA, Gustav Fischer Verlag, 84 pp.

REISZ, R. 1980. The Pelycosauria: A review of phylogenetic relationships, pp. 553–592. *In* A. L. Panchen (ed.), The Terrestrial Environment and the Origin of Land Vertebrates, London and New York, Academic Press.

REISZ, R., M. J. HEATON, AND B. R. PYNN. 1982. Vertebrate fauna of the Late Pennsylvanian Rock Lake Shale near Garnett, Kansas: Pelycosauria. J. Paleontol., **56**: 741–750.

ROMER, A. S. 1946. The primitive reptile *Limnoscelis* restudied. Am. J. Sci., **244**: 151–188.

———. 1956. The Osteology of the Reptiles. Chicago and London, University of Chicago Press, 772 pp.

ROMER, A. S., AND L. I. PRICE. 1940. Review of the Pelycosauria. Geol. Soc. Am. spec. Pap. No. 28, 538 pp.

WATROUS, L. E., AND Q. D. WHEELER. 1981. The out-group comparison method of character analysis. Syst. Zool., **30**: 1–11.

WILLISTON, S. W. 1911. American Permian Vertebrates. Chicago, University of Chicago Press, 145 pp.

MUS. COMP. ZOOL.
LIBRARY
MAR 18 1985
HARVARD
UNIVERSITY

B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 29 APRIL 1983 NUMBER 474

RUTHIROMIA ELCOBRIENSIS, A NEW PELYCOSAUR FROM EL COBRE CANYON, NEW MEXICO

DAVID A. EBERTH[1] AND DONALD BRINKMAN[2]

ABSTRACT. *Ruthiromia elcobriensis*, a new genus and species of pelycosaur from the Permo-Carboniferous redbeds of El Cobre Canyon, New Mexico, is based upon an articulated portion of the vertebral column, partial appendicular skeleton, and associated vertebral and cranial fragments. *Ruthiromia* is tentatively included within the Varanopseidae on the basis of postcranial characters. It is distinguished from all other varanopseids by its larger size, pinched-in lumbar centra, and massively developed delto-pectoral crest.

INTRODUCTION

The Permo-Carboniferous, Cutler formation redbeds of El Cobre Canyon, New Mexico, have yielded a unique assemblage of fossil tetrapods. El Cobre Canyon, near Abiquiu, New Mexico, is a large box canyon that has been sporadically prospected by collectors and paleontologists since the late 1870's. The fossil fauna and flora, known from both the canyon walls and floor, was most recently reviewed by Fracasso (1980).

In 1965 A. Lewis and S. Olsen collected the larger part of the postcranial skeleton and disarticulated cranial fragments of a

[1]Department of Geology, University of Toronto, Toronto, Ontario, Canada, M5T 1R7.

[2]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. Present Address: Tyrrell Museum of Paleontology, Box 7500, Drumheller, Alberta, Canada, TOJ OYO.

pelycosaur from the west wall of the canyon. The specimen, referred to *Ophiacodon navajovicus,* remained largely unprepared in the collections at the Museum of Comparative Zoology at Harvard University until the spring of 1980 when the authors undertook a study of the specimen (MCZ 3150). Preparation and study of the material has shown that while it is clearly a pelycosaur, it is unassignable to *Ophiacodon.* It is here described as a new genus and species, a primitive member of the family Varanopseidae.

SYSTEMATIC PALEONTOLOGY

Class: Reptilia
Order: Pelycosauria
Family: Varanopseidae
Genus: *Ruthiromia* gen. nov.
Type species: *Ruthiromia elcobriensis* gen. et sp. nov.

Etymology: Named in honor of Ruth Romer.

Diagnosis: A large varanopseid distinguished from all other members of the family in the following features: linear measurements approximately 30 percent greater than those of *Varanodon,* previously the largest known varanopseid; the first eight centra directly anterior to the pelvis deeply pinched-in laterally, just below the level of the notochordal pit, giving the centra an hour-glass appearance when seen in cross section; each of the eight centra displays a broad rounded ventral surface; the delto-pectoral crest of the humerus is massively developed and continues distally as a sharp ridge below the area of pectoralis muscle insertion; the neck of the astragulus represents 35 percent of the total height of that element.

Ruthiromia elcobriensis differs from *Varanops brevirostris* in having a keeled angular in the region of the articular; a large medial process of the articular positioned farther forward than in the latter genus; and a low bladed ilium. *Ruthiromia elcobriensis* differs from *Aerosaurus greenleeorum* in not exhibiting the excavated anterior lip in its anterior dorsal vertebrae. *Ruthiromia elcobriensis* differs from *Aerosaurus wellesii* in retaining a short paroccipital process and two sacral ribs.

Ruthiromia elcobriensis gen. et sp. nov.
(Figs. 2–8, 9–5)

Etymology: Named in reference to El Cobre Canyon, the type locality.

Diagnosis: Same as for the genus.

Holotype (MCZ 3150): An articulated, partial vertebral column, pelvis and right hind limb found in close association with disarticulated elements. All material is considered to represent a single individual. Material includes: an occipital fragment including supraoccipital and opisthotic; a left quadrate fragment in articulation with a partial quadratojugal and squamosal; the posterior portion of the left mandible, the atlas centrum and axis intercentrum; a cervical rib; four disarticulated dorsal vertebrae; one disarticulated neural arch; one partial neural spine; articulated posterior axial elements including the last seven presacral vertebrae, two sacral vertebrae and five caudal vertebrae; right and left partial scapulacoracoids; a complete right pelvic girdle; a partial left pelvic girdle including pubis, ischium and a partial ilium; a right humerus; a right femur; a left proximal femur; a right tibia, fibula, tarsus, and pes.

Type Locality and Age: Cutler Formation, Lower Permian. Collected from the fluvial redbeds in the west wall of El Cobre Canyon. Specific collecting site unknown.

METHODS

Although comparisons of *Ruthiromia elcobriensis* with other pelycosaur taxa have been performed in line with phylogenetic systematic principles, a few words on polarity determinations within the pelycosaurs are in order. Following Brinkman and Eberth (1983), we accept a very primitive position for the varanopseids within the paraphyletic taxon Pelycosauria (Fig. 16). Thus any pelycosaur taxon may appear closely related to the varanopseids, caseids, and eothyridids simply by exhibiting primitive characters. To guard against the use of symplesiomorphy in establishing the affinities of *Ruthiromia elcobriensis,* we have evaluated character state polarities within the context of what we consider to be a generally accepted view of amphibian/reptile relationships. In this paper

we adopt the classification of Carroll (1969) modified by Heaton (1980) (Fig. 1). It is by reference to the Diadectomorpha (including *Tseajaia, Limnoscelis,* and *Diadectes*) as the closest sister taxon of reptiles and the relative distribution of character states in reptiles that we determine character polarity in primitive pelycosaurs and specifically *Ruthiromia elcobriensis.*

DESCRIPTION AND COMPARISON

Skull: A small fragment of the left side of the occiput is preserved (Fig. 2A,B). The tall anteroposteriorly flattened paroccipital process extends directly laterally beneath the posttemporal fenestra and terminates in a convex, thin edge as in *Varanops* and *Aerosaurus wellesii.* No trace of a suture between the opisthotic and supraoccipital is visible. In posterior view, unfinished lateral edges of the supraoccipital suggest that the absence of lateral processes is a result of incomplete preservation. The anterior surface of the occipital fragment displays a small gap between the anterior surface of the supraoccipital and an anteromedial continuation of the opisthotic. No notch for the trigeminal is visible however, and it appears that only the corner of the braincase in this region is perserved.

As in pelycosaurs and primitive reptiles generally, the quadrate is quite tall (Fig. 3A,B,C). Both condyles are oriented with their long axes anteromedially, the medial condyle being the more elongate. A saddle-shaped concavity occurs between the two condyles. Fragmentary bone lateral to the posterior edge of the element probably represents the squamosal and a portion of the quadratojugal. Distal extremities are not preserved. No stapedial recess is discernible on the medial surface of the quadrate.

The posterior portion of the left mandible (Fig. 4 A,B,C), includes the articular, part of the surangular, angular and possibly prearticular and measures 7.7 cm long. The condylar recesses of the articular are in the horizontal plane. The articular has a large triangular, medially projecting process whose medial apex is in line with or slightly ahead of the posterior margin of the Meckelian trough and well ahead of the condylar recesses. This is closely comparable to the condition seen in *Aerosaurus wellesii.* In *Varanops* the medial apex of the process is located just slightly anterior to the condylar recesses. In the area of the articular, the angular is keeled and compares quite well with *A. wellesii* and *Varanodon. Varanops* differs in

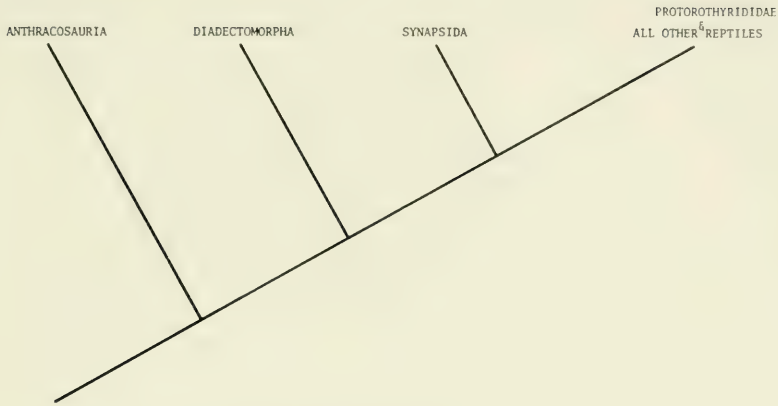


Figure 1. Cladogram depicting relationships of taxa closely involved in the amphibian/reptilian transition. Derived from Carroll (1969) and modified by Heaton (1980).

Figure 2. *R. elcobriensis,* MCZ 3150. A. Posterior view of left opisthotic/supraoccipital fragment. B. Anterior view of the same. Scale equals 1 cm.

Abbreviations: op, opisthotic; st, supratemporal.

having an angular that is gently rounded in this portion of the jaw. The posterior limit of a medial fenestra is preserved at the anterior most portion of the mandibular fragment and appears to be bounded by the angular and the prearticular.

Axial Skeleton: The vertebral column is known from an articulated series of 14 vertebrae and five disarticulated vertebrae. All regions are represented, but only the atlas is present from the cervical region. The centra are clearly larger than their counterparts in other varanopseid taxa (Table 1) and appear to be relatively shorter than those of *Varanops* and *A. greenleeorum* (Table 2).

Figure 3. *R. elcobriensis,* MCZ 3150. A. Anterior view of left quadrate/squamosal/quadratojugal fragment. B. Medial view of the same. C. Ventral view of the same. Scale equals 1 cm.

Abbreviations: q, quadrate; sq, squamosal.

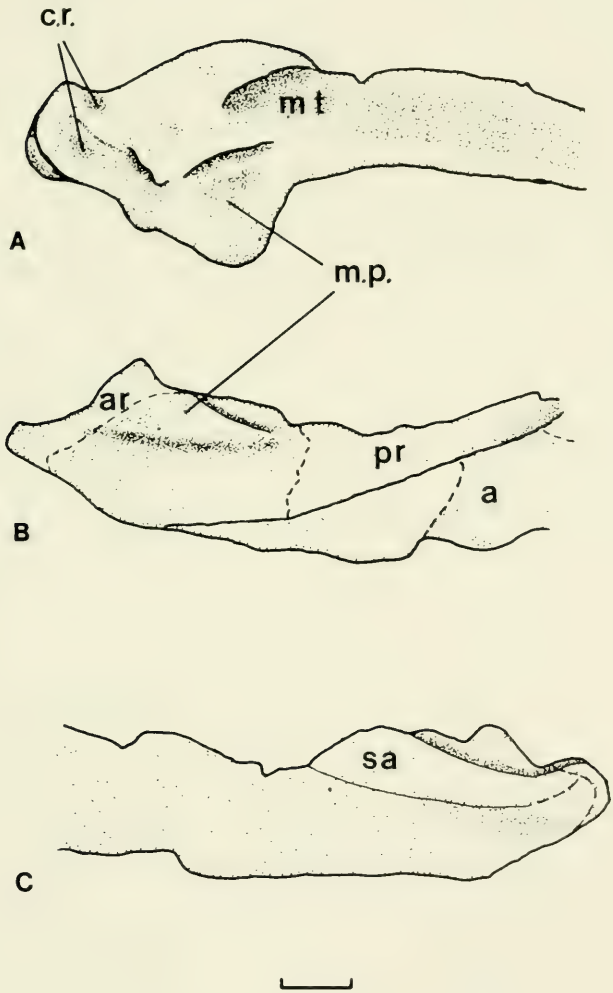


Figure 4. *R. elcobriensis,* MCZ 3150. A. Dorsal view of left mandibular fragment. B. Medial view of the same. C. Lateral view of the same. Scale equals 1 cm.

Abbreviations: a, angular; ar, articular; cr, condylar recesses of articular; mp, medial process of the articular; mt, Meckelian trough; sa, surangular.

Table 1. Comparative linear measurements (mm) within the Varanopseidae.*

ELEMENT		Ruthiromia	Varanodon	Varanops	A. wellesi	A. greenleeorum
Vertebrae						
Atlas	L.	17.1				
	A.H.	18.1				
	A.W.	15.5				
Ant. dorsal	L.	17.0+		16.0	10.5	13.0
	A.H.	19.0				
	P.H.	18.0		12.0		10.0
Mid. dorsal	L.	22.0		14.0	11.4	
	A.H.	21.5			-	
	P.H.	20.5		14.0	8.1	
	A.W.	20.0				
	P.W.	20.0		12.5	8.9	
Post. dorsal	L.	17.5		15.0		14.0
	A.H.	17.0+				
	P.H.	18.5		14.0		12.0
	A.W.	18.0				
	P.W.	17.0		13.0		12.0

Spine	H.	34.5		23.0	18.0	
Humerus	L.	105.6	81.0	72.0	53.0	
	PR.W.	52.4	35.0	35.0	22.3	38.0
Ilium	L.	88.5		52.0	34.7	
	NECK	25.2		24.0	13.0	22.0
	BASE	46.4		38.0	23.6	34.0
Pubis	L.	60.0		48.0		
Ischium	L.	75.0		58.0		
Femur	L.	116.5		87.0	62.5	
	PR.W.	40.0		30.0	17.0	
	D.W.	43.5		30.0		
	SHAFT	11.7				
Tibia	L.	80.0		72.0	52.4	
Fibula	L.	72.0+		75.0	64.0	
	PR.W.	27.0		18.0	12.8	
	SHAFT	6.4				
Astragulus	H.	31.5				
	NECK H.	11.1				
	W.	22.0				

Table 1. Comparative linear measurements (mm) within the Varanopseidae.* *(continued)*

ELEMENT		*Ruthiromia*	*Varanodon*	*Varanops*	*A. wellesii*	*A. greenleeorum*
Calcaneum	H.	36.5				
	W.	28.7	—	—	—	—
1st Mtt.	L.	11.5				
	SHAFT	10.4				
	PR.W.	13.3				
	D.W.	12.5				
2nd Mtt.	L.	20.0				
	SHAFT	6.0				
	PR.W.	9.4				
	D.W.	10.0				
3rd Mtt.	L.	30.0				
	SHAFT	4.5				
	PR.W.	11.5				
	D.W.	13.5				
4th Mtt.	L.	38.5				
	SHAFT	6.4				
	PR.W.	15.0				
	D.W.	16.5				

*Abbreviations: A.H., anterior height; A.W., anterior width; Base, width of base of ilium; D.W., distal width; H., height; L., length; Neck, width of neck of ilium; P.H., posterior height; P.W., posterior width; PR.W., proximal width; Shaft, minimum thickness of shaft; W., width.

Table 2. Element ratios within the Varanopseidae.*

ELEMENT RATIO		Ruthiromia	Varanodon	Varanops	A. wellesii	A. greenleeorum
Mid. dorsal						
Vertebra	P.W. L.	0.91		0.78		0.86
	P.W./Spine H.	0.58		0.54	0.49	
Humerus	PR.W./L.	0.50	0.43	0.49	0.42	
Ilium	NECK L.	0.28		0.46	0.37	
	BASE L.	0.52		0.73	0.68	
Femur	PR.W./L.	0.34		0.34	0.27	
	D.W. L.	0.37		0.34		
Humerus Femur	(L.)	0.91		0.83	0.85	
Tibia/Femur	(L.)	0.69		0.83	0.84	

*Abbreviations: See Table 1.

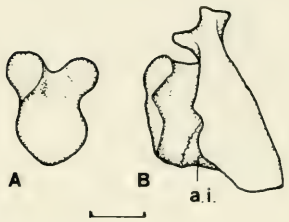


Figure 5. *R. elcobriensis,* MCZ 3150. A. Anterior same and right cervical rib. Scale equals 1 cm.

Abbreviations: ai, axis intercentrum.

A small block of matrix contains the atlas centrum and the axis intercentrum as well as a spatulate cervical rib (Fig. 5A,B). The atlas centrum is fully ossified and is exposed ventrally. The axis intercentrum is a large crescentic element fused to the posterior surface of the atlas centrum. Although the atlas centrum is visible ventrally, it is the axis intercentrum that is more prominent, contributing to more than 50 percent of the ventral surface. The condition in *Varanops* is like that in *Ruthiromia.* The condition in *Varanodon, A. greenleeorum,* and *A. wellesii* is unknown.

The head of the cervical rib exhibits separate capitular and tubercular processes. The shaft is expanded anteroposteriorly as a spatulate convex blade.

A disarticulated anterior dorsal vertebra includes the centrum and partial neural arch and displays an anterolaterally projecting diapophysis that extends 6.8 mm from the unexpanded neural arch (Fig. 6). The ventral surface of the centrum is sharply keeled. This is the typical morphology of all varanopseids with the exception of *A. greenleeorum.* There, the anterior lip of the centrum is deeply recessed to receive the intercentrum and the ventral surfaces are never as strikingly keeled. The floor of the neural canal is not ossified, resulting in a deep excavation which extends nearly to the mid-height of the centrum as in *Varanops* and *A. greenleeorum.* The articulating surface of the zygapophysis is slightly inturned and forms an angle of 20 degrees to the horizontal.

The three remaining disarticulated dorsal vertebrae (Fig. 7) can be arranged relative to one another but position in the column is

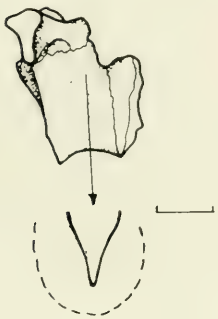


Figure 6. *R. elcobriensis,* MCZ 3150. Left lateral view of anterior dorsal vertebra and a cross section through the mid-length. Scale equals 1 cm.

uncertain. All three display a small pit on the lateral surface of the centrum wall at mid-height. The more anterior of the three is keeled, although not as sharply as the anterior dorsal vertebra just described. The ventral surface of the centrum displays three closely set ridges extending anteroposteriorly. In *Varanops* comparable ridges occur on the 22nd presacral vertebra (Fig. 9).

The second vertebra retains a laterally projecting diapophysis that extends 7 mm from the neural arch. The ventral surface is gently rounded, however, and shows no trace of a keel or ridges.

The third vertebra differs from the preceding two in that the ventral surface of the centrum is more broadly rounded.

Neural arch excavations are present on the third vertebra and extend anteroventrally and open onto the surface of the neural arch between the diapophyses and the anterior zygapophyses. The diapophysis projects posterolaterally and measures 5 mm from the surface of the neural arch. The articulating surface of the zygapophysis appears nearly horizontal. The orientation of the diapophysis and the smoothly rounded ventral edge of the centrum suggest that this vertebra was a lumbar.

Although the last seven presacral vertebrae are in articulation (Fig. 8), only the first four of the series are preserved well enough to merit discussion. As in the preceding vertebrae, each displays a small pit in the lateral wall of the centrum at mid-height. The lateral

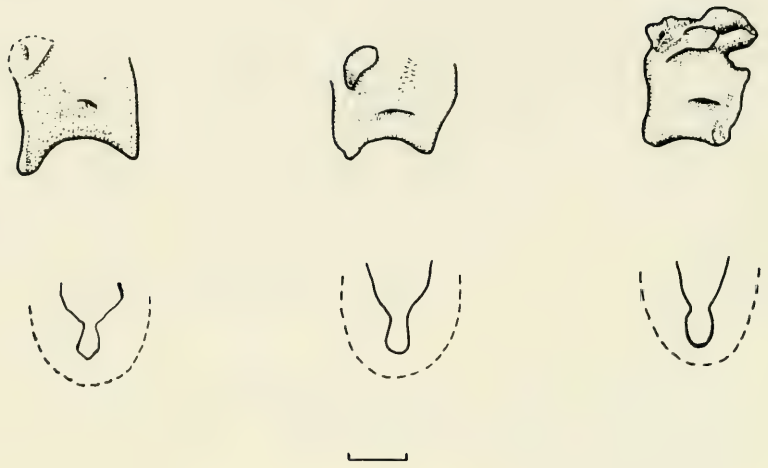


Figure 7. *R. elcobriensis*, MCZ 3150. Left lateral views and cross sections of three dorsal centra arranged with the anterior most to the left. Scale equals 1 cm.

walls of the centra are strongly concave and the ventral surfaces are broadly rounded giving the centra an hour-glass shape in cross section. This condition is termed pinched-in. No other varanopseid displays this condition in the posterior dorsal centra. *Varanops* displays broadly rounded ventral surfaces on its last four presacral vertebrae (Fig. 9), but there is no indication of pinching-in or pitting of the lateral walls of the centra. A posterior dorsal vertebra of an immature *A. wellesii* (UCMP 20096?) displays a pit in the lateral wall of the centrum, but lacks the pinched-in condition.

The neural arches of the last three presacral vertebrae are deeply excavated at the level of the articular surfaces of the zygapophyses.

All neural spines in this articulated series are imperfectly preserved and show only the primitive condition of being laterally compressed. The centra of all of the vertebrae posterior to the third vertebra of the series are either inaccessible or poorly preserved.

A disarticulated neural arch with a complete neural spine is poorly preserved but shows that the spine is relatively lower in height than those of *Varanops* and *A. wellesii* (Table 2).

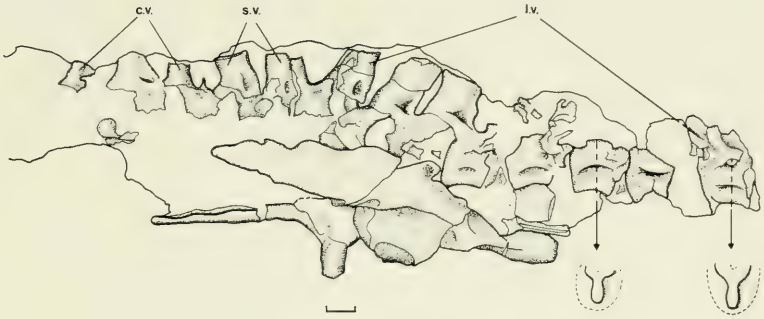


Figure 8. *R. elcobriensis,* MCZ 3150. Right lateral view of articulated lumbar, sacral, proximal caudal vertebrae and pelvis. Scale equals 1 cm.

Abbreviations: cv, caudal vertebrae; lv, lumbar vertebrae.

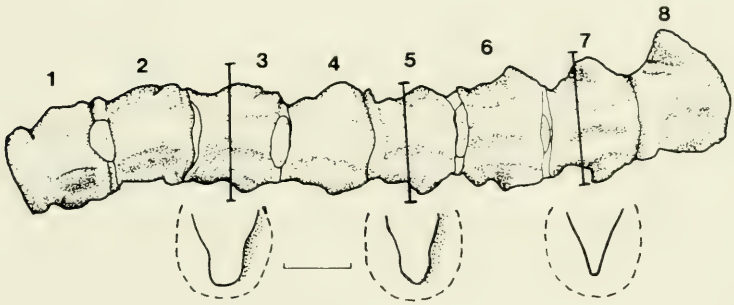


Figure 9. *Varanops brevirostris,* MCZ 1926. Ventral view and cross sections of last eight presacral vertebrae. Anteriormost to the right. Scale equals 1 cm.

The neural arches of the sacral vertebrae are deeply excavated above the articular surfaces of the zygapophyses. Two poorly preserved sacral ribs are present. *Aerosaurus wellesii* has three sacral ribs and appears to be unique in this feature within the varanopseids (Langston and Reisz, 1981).

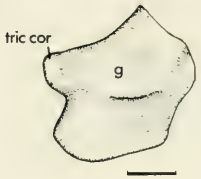


Figure 10. *R. elcobriensis*, MCZ 3150. Lateral view of right scapulocoracoid fragment. Scale equals 1 cm.

Abbreviations: g, glenoid; tric cor, process for the coracoid head of the M. triceps.

The first caudal vertebra is distorted and thus appears wider than the more posterior caudals. The neural spines of the caudal vertebrae are smaller than those of the sacral or presacral vertebrae and appear almost triangular in lateral aspect. All of the five articulated caudals display excavated neural arches.

Appendicular Skeleton: Fragmentary right and left scapulocoracoids are preserved. Both display at least a portion of the glenoid and a well-developed process for the origin of the coracoid head of the *M. triceps* (Fig. 10). In primitive fashion the glenoid is not raised above the surface of the coracoid and continues back onto the triceps process. Similar conditions exist elsewhere in all known varanopseids.

The right humerus is well preserved (Fig. 11) and has proportions conformable with those present in *Varanops* (Table 2). *Varanodon* and *A. wellesii* have a proportionately narrower proximal ends. The proximal end of the humerus displays a stout *M. latissimus* tubercle. This tubercle is poorly ossified in *Varanops* and *A. wellesii* but is well ossified in *A. greenleeorum* and most other pelycosaurs. The proximal surface in the region of the deltopectoral crest exhibits two well-developed parallel ridges with a depression between them. Such a condition exists in *A. greenleeorum* and elsewhere in pelycosaurs only in caseids (Brinkman and Eberth, 1983). A feature of the humerus not seen in other varanopseid taxa is that of a massively developed delto-pectoral crest that continues distally as a sharp ridge. This distal extension is so prominent that the entire region appears almost square in anterior aspect. Romer and Price (1940) distinguished *A. greenleeorum* partly on the basis of a well-

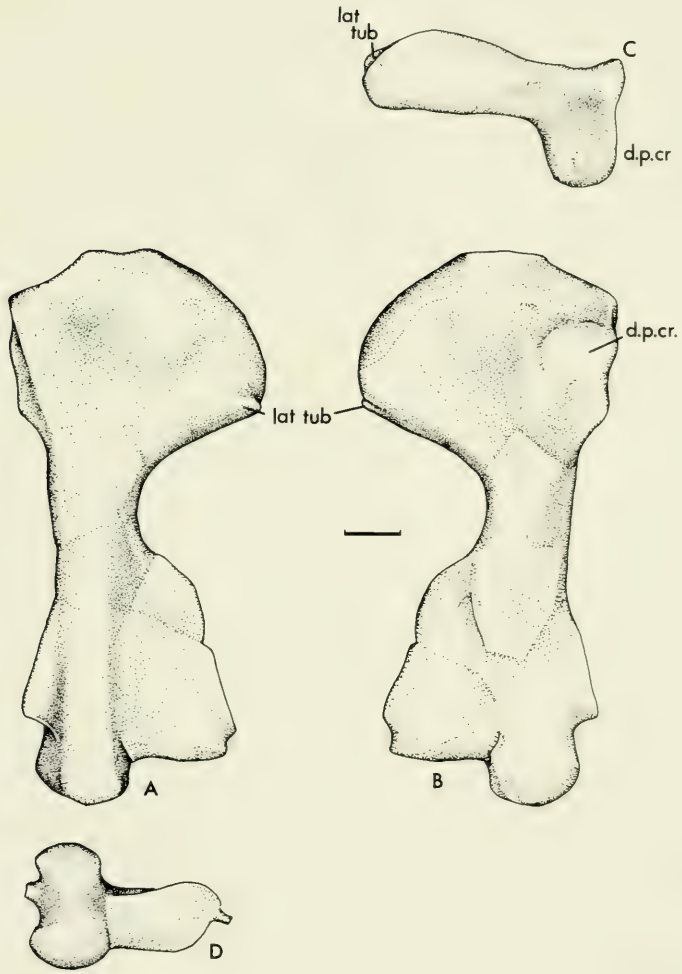


Figure 11. *R. elcobriensis,* MCZ 3150. A. Proximal dorsal view of left humerus. B. Proximal ventral view of the same. C. Proximal view of the same. D. Distal view of the same. Scale equals 1 cm.

Abbreviations: dpcr, delto-pectoral crest; lat tub, latissimus tubercle.

developed deltopectoral crest. Direct comparison indicates that *A. greenleeorum* lacks the distal ridge. A strong ectepicondyle occurs distally and is well separated from the partially preserved supinator process. Much of the entepicondyle is missing, and the position of the entepicondylar foramen is uncertain. Distoventrally, a large radial condyle is preserved.

The right pelvis is well preserved and has been completely prepared laterally and ventrally. The medial surface of the ilium has also been prepared. The pelvis is quite primitive in general structure, having a posteriorly projecting iliac blade and a solid puboischiadic plate. The ilium (Fig. 12A,B) is triangular in lateral aspect. It becomes wider and longer ventrally where it forms the dorsal portion of the acetabulum. The elongate, triangular posterior process is low as in *A. wellesii* and *Varanops* but appears longer exhibiting lower base/length and neck/length proportions than in those two species (Table 2). A small anterior projection of the ilium is poorly preserved. In medial aspect (Fig. 12B) a ridge bisects the length of the posterior process and appears conformable with that present in all other varanopseids. The pubis is primitively short and ends anteriorly in a slightly thickened knob (Fig. 12D). In lateral aspect, the dorsal margin of the pubis is thickened and appears concave. A poorly preserved bump on the lateral surface, directly anterior to the acetabulum, may be a pubic tubercle. A pubic tubercle is unknown in other varanopseid taxa, but is found in the ophiacodontids *Clepsydrops* and *Varanosaurus* as well as caseids and edaphosaurids. The widespread occurrence of a pubic tubercle in pelycosaurs as well as many cotylosaurs suggests that it is primitive.

The ischium is complete and also displays a slightly thickened dorsal margin in lateral aspect (Fig. 12C). The ischiadic plate is thin and meets its counterpart of the left side in the mid line. The ischium appears conformable with the known morphology of that same element in other varanopseids and ophiacodontids.

The right femur is complete (Fig. 13) although a small portion of the proximal end is broken off and remains in articulation with the acetabulum, obscuring the morphology of the latter. The proximal end of the left femur is also preserved. Measurements and proportions are listed in Tables 1 and 2 respectively. No significant differences in femoral proportions between *Ruthiromia* and other varanopseid taxa are apparent. In anterior aspect, the proximal end

Figure 12. *R. elcobriensis,* MCZ 3150. A. Lateral view of right ilium. B. Medial view of the same. C. Ventrolateral view of right ischium. D. Ventrolateral view of right pubis. Scale equals 1 cm.

Abbreviation: pt, pubic tubercle.

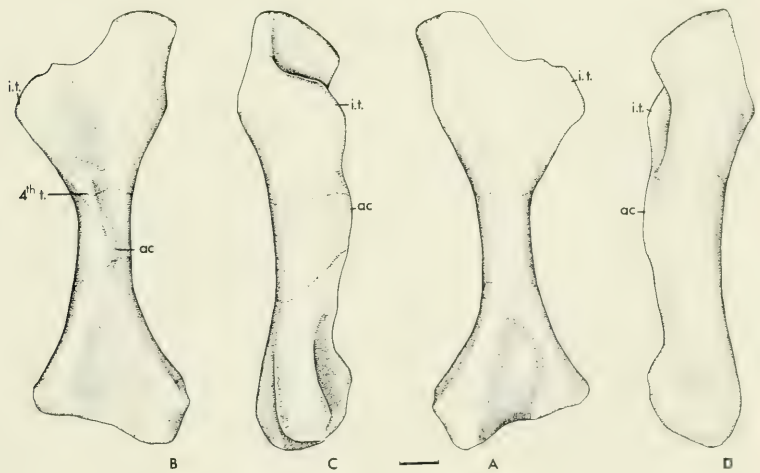


Figure 13. *R. elcobriensis,* MCZ 3150. A. Dorsal view of right femur. B. Ventral view of the same. C. Posterior view of the same. D. Anterior view of the same. Scale equals 1 cm.

Abbreviations: ac, adductor crest; 4th t, 4th trochanter; it, internal trochanter.

of the right femur displays a large, tall internal trochanter well set off from the thickened proximal surface of the femur. *Varanops* (the only varanopseid where this condition can be compared) does not exhibit such a well-developed internal trochanter. The intertrochanteric fossa is extensive, occupying about a third of the length of the femur as in most non sphenacodontid pelycosaurs. A large knob marks the point of attachment of the M. pubo ischio femoralis internus. The distinct, although small, fourth trochanter is present just distal to the intertrochanteric fossa. A prominent, well-ossified adductor crest extends across the ventral surface of the element to the fibulad edge. The crest is relatively larger than in any other varanopseids and appears to be a primitive feature. In cross section the shaft appears tear drop-shaped, in contrast to *Varanops* where a cross section appears oval. In dorsal view, the two well-developed ossified tibial condyles are well separated by a deep intercondylar fossa. Their dorsal surfaces are essentially flat, and their articular surfaces are oriented ventro laterally.

In dorsal view (Fig. 14) the right tibia and fibula have straight external and concave internal edges. The fibula is slightly shorter than the tibia (Table 1). The lateral femoral cotyle of the tibia is not strongly compressed. Sharp ridges are present on the lateral and medial edges of the distal half of the bone. The proximal end of the fibula is damaged, so the extent of the dorsal tubercle is unknown. The distal end is wide mediolaterally and compressed dorsoventrally. Similar overall conditions are seen to exist in all varanopseids.

Eight elements are present in the tarsus: the astragulus, calcaneum, a centrale and five distal tarsals (Fig. 15). The astragulus (Fig. 15A,B) is L-shaped and supports both the tibia and fibula. The neck of the astragulus is elongate and contributes to 35 percent of the height of the element; it thus appears more like that of a sphenacodontid than all other known varanopseids. It is unclear at present whether this is a primitive or derived feature. In contrast to sphenacodontids however, no tubercle is present on the ventral surface of the astragulus medial to the arterial groove. The calcaneum (Fig. 15A,B) is primitive in being wide and having a convex lateral edge when seen in dorsal view. In contrast to the varanopseid genera *A. wellesii* and *Varanops,* the element is much taller than it is wide.

The single centrale (Fig. 15C) is a small element with a limited area of finished bone on its dorsal surface. The largest of the distal

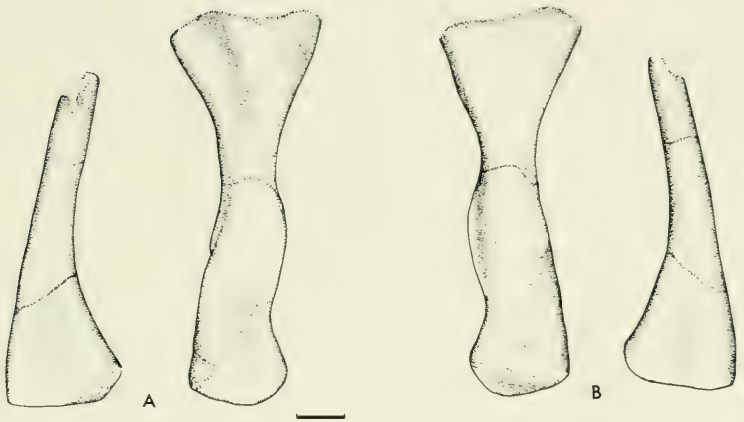


Figure 14. *R. elcobriensis*, MCZ 3150. A. Dorsal view of right tibia and fibula. B. Ventral view of the same. Scale equals 1 cm.

tarsals is the fourth. In dorsal view (Fig. 15C) it is essentially pentagonal in contrast to the rectangular fourth distal tarsal of *A. wellesii* and *Varanops*. The fourth distal tarsal also shares an equal contact with the astragulus. The first and third distal tarsals are subequal in size and the second is slightly smaller than these. This is also the case in *Varanops* and *A. wellesii*. The metatarsals increase in length from first to fourth (Table 1). The first metatarsal is supported entirely by the first distal tarsal. In dorsal view, the second and third articulate with the distal tarsal of the same number. In ventral view (Fig. 15D) each of these metatarsals is supported by both the distal tarsal of the same number and the laterally adjacent distal tarsal. The fourth metatarsal is longer than the combined length of the first metatarsal and digit. This condition is seen developed to a greater degree in *Varanops* and to a lesser degree in *A. wellesii* and occurs elsewhere within the pelycosaurs only in *Varanosaurus* and *Ophiacodon mirus*. The first toe has a clawlike terminal phalanx. The remaining toes are incompletely preserved or not present.

In overall appendicular proportions (Table 2), *Ruthiromia elcobriensis* appears more primitive than any other varanopseid in having a humerus and femur of subequal lengths and a lower tibia/femur ratio.

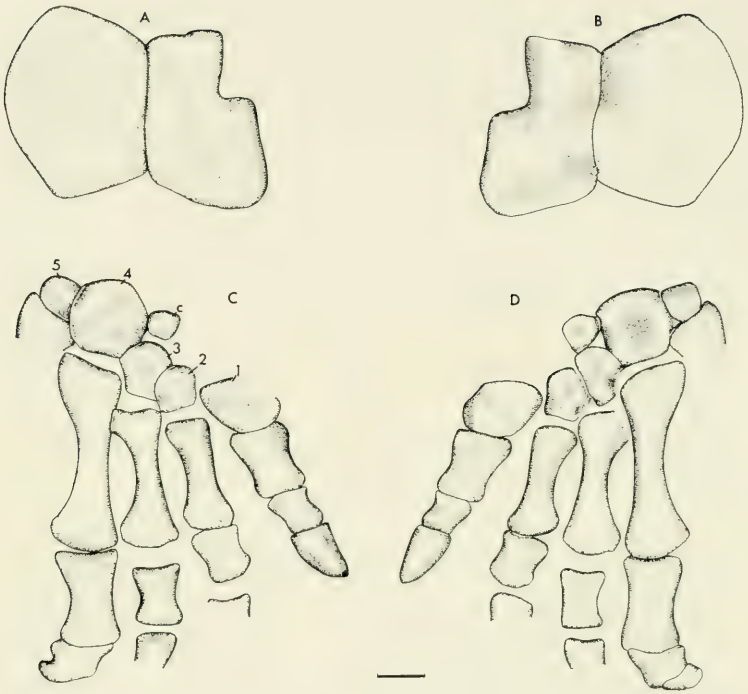


Figure 15. *R. elcobriensis,* MCZ 3150. A. Dorsal view of right astragalus/calcaneum complex. B. Ventral view of the same. C. Dorsal view of right pes. D. Ventral view of the same. Scale equals 1 cm.

Abbreviation: c, centrale.

DISCUSSION

Ruthiromia elcobriensis is considered a pelycosaur on the basis of the combined, derived characters (within reptiles) of excavated neural arches, keeled mid-dorsal vertebrae, a strongly developed process for the coracoid head of the triceps and a keeled angular in the region of the articular. These constitute a suite of characters which is found only within the pelycosaurian families Varanopseidae and Sphenacodontidae.

The Varanopseidae is currently defined by cranial characters (Langston and Reisz, 1981), yet shows a unique combination of two derived, postcranial characters: excavated neural arches and the

presence of a shallow fossa on the proximal surface of the deltopectoral crest (Brinkman and Eberth, 1983). *Ruthiromia elcobriensis* is tentatively assigned to the Varanopseidae on the basis of displaying these same characters. Following the cladistic classification of Brinkman and Eberth (1983, Fig. 16) for the better known pelycosaur genera, the derived character of excavated neural arches is thought to have developed either two (Fig. 16A) or three (Fig. 16B) times. All varanopseid and sphenacodontid taxa, where postcranial material is available, show excavated neural arches. Within the edaphosaurids an undescribed specimen (E2) from the Pennsylvanian of Kansas shows this condition (R. Reisz, personal communication). Within this context and assuming parsimony, four equally correct positions denoting propinquity of descent of *Ruthiromia elcobriensis* may be depicted in a cladogram (Fig. 16C).

Position 1 places *Ruthiromia elcobriensis* as a member of the varanopseids in the clade including *Varanops*/*Aerosaurus* and *Casea*. This clade is united by the derived morphology of the proximal surface of the humerus in the region of the delto-pectoral crest. As described above, *Ruthiromia elcobriensis* shares this same morphology.

Relationships indicated by positions 2, 3, and 4 each necessitate reversals of those characters at nodes (c), (c,d,e) and (c,d) respectively. The clade including *Ophiacodon, Edaphosaurus,* and *Dimetrodon* is defined by the shared presence of a rodlike paroccipital process with a socket on the ventral surface for contact with a distinct dorsal process of the stapes, a concave ventral margin of the cheek and a single postparietal (node c). *R. elcobriensis* has a narrow paroccipital process that shows no evidence of a socket along its ventral edge for contact with a dorsal stapedial process. A relationship indicated by position 2 therefore involves the reversal of this character. Other regions are not preserved in the holotype. Similarly, *Ruthiromia elcobriensis* does not show the derived characters of the twisted prearticular and ventromedial projecting pterygoideus process which partially define the clade consisting of *Edaphosaurus* and *Dimetrodon* (node d). In this case, a total of three reversals (reversal at both c and d) is necessary to explain the relationship indicated by position 4. Finally, the relationship indicated by position 3 necessitates the reversals listed above as well as reversals of the autapomorphic characters that define the Edaphosauridae and

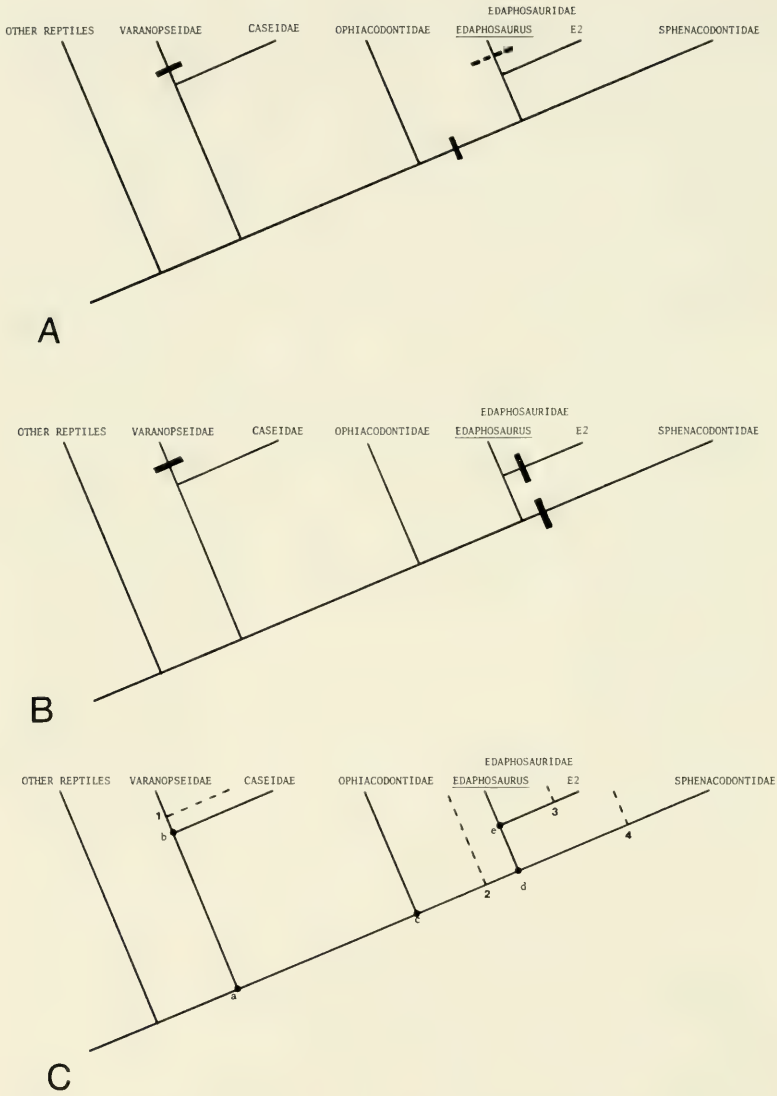


Figure 16. Cladograms depicting relationships of pelycosaur families. Adopted and modified from Brinkman and Eberth (1983). A&B. Two equally parsimonious hypotheses for the appearance and distribution of excavated neural arches in pelycosaurs. Solid bars represent those points where excavated neural arches are exhibited. Dashed bar represents point of character loss. C. Four equally correct positions for *Ruthiromia* on the basis of the derived character of excavated neural arches.

are not seen in *Ruthiromia elcobriensis* (elongate neural spines with lateral tubercles, low position of the jaw articulation relative to the tooth row). Clearly, the most parsimonious course to take is to tentatively place *Ruthiromia elcobriensis* among the Varanopseidae as a primitive member of that family. The tentative nature of this placement reflects both the lack of diagnostic cranial material in the type and the employment of a combination of derived postcranial characters, none of which can serve alone as an autapomorphic character of the family Varanopseidae.

Ruthiromia appears to be more closely allied with *A. wellesii* in sharing the unique character of the forwardly placed medial process of the articular and the keeled angular.

Ruthiromia shares only primitive characters with *Varanops* and appears similar in retaining a laterally projecting paroccipital process and in having only two sacral vertebrae.

The morphology of the lumbar vertebrae and more specifically the position in the column where keeled vertebrae first appear is more difficult to assess. The seven articulated presacral vertebrae of *Ruthiromia* show no signs of possessing keels and all retain a gently rounded ventral surface. The inclusion in the holotype of one disarticulated lumbar (posterior dorsal) with a similarly unkeeled ventral surface places the minimum location for the transitional vertebra at a position nine vertebrae in front of the pelvis. In addition, a significant difference in diapophysis orientation between the transitional vertebra and the isolated lumbar (lateral vs. postero lateral respectively) warrants placement of the transitional vertebra even further forward in the column. *Varanops* develops a fully keeled vertebra six vertebrae ahead of the pelvis (Fig. 9). The fifth is transitional, displaying three parallel ridges along the ventral surface. The only fully prepared vertebrae known from *A. wellesii* that can be placed in the column with certainty are those nine and ten positions ahead of the pelvis. These show keeled ventral surfaces. No idea concerning the initial position of keeled vertebrae can be determined in either *A. greenleeorum* or *Varanodon,* but *A. greenleeorum* does not appear to develop strong keels of the sort seen in the one known anterior dorsal of *Ruthiromia* anywhere in its column. *Ruthiromia* similarly does not share with *A. greenleeorum* the condition of the deeply recessed anteroventral lips of the anterior dorsals. Keeled lumbar vertebrae are considered an advanced character state (Romer

and Price, 1940). *Ruthiromia* appears more primitive than either *Varanops* or *A. wellesii* in displaying a greater number of unkeeled vertebrae in the presacral region of the vertebral column.

In summary, *Ruthiromia elcobriensis* represents a varanopseid which is very primitive postcranially, with some unique vertebral specializations. Cranially, it shows some of the same advanced specializations seen in *A. wellesii* and perhaps *Varanodon.*

ACKNOWLEDGMENTS

The authors wish to express their gratitude and appreciation to Robert Reisz for his many valuable comments and criticisms as well as the technical assistance that he provided during the preparation of this manuscript. Although his help must be regarded as a crucial factor in the production of this paper, the authors assume full responsibility for any errors that might be present.

Travel and research expenses were covered, in part, by a Schmitt Fund research grant provided by the Field Museum of Natural History, Chicago.

LITERATURE CITED

Brinkman, D., and D. Eberth. 1983. The interrelationships of Pelycosaurs. Breviora Mus. Comp. Zool., No. 473.

Carroll, R. L. 1969. The origin of reptiles, pp.1–44. *In* A.d'A. Bellairs *et al.* (eds.), Biology of the Reptilia. New York, Academic Press, 373 pp.

Fracasso, M. A. 1980. Age of the Permo-Carboniferous Cutler Formation vertebrate fauna from El Cobre Canyon, New Mexico. J. Paleontol., **44**: 156–163.

Heaton, M. J. 1980. The Cotylosauria: A reconsideration of a group of archaic tetrapods, pp. 497–551. In. A. L. Panchen (ed.), The Terrestrial Environment and the Origin of Land Vertebrates. Systematics Assoc. Spec. Vol. No. 15, London, Academic Press, 633 pp.

Langston, W. Jr., and R. R. Reisz. 1981. *Aerosaurus wellesii,* new species, a varanopseid mammal-like reptile (Synapsida: Pelycosauria) from the lower Permian of New Mexico. J. Vertebr. Paleontol., **1**(1): 73–96.

Olson, E. C. 1965. New Permian vertebrates from the Chickasha Formation in Oklahoma. Oklahoma Geol. Surv. Circ. No. 70, 70 pp.

Romer, A. S., and L. I. Price. 1940. Review of the Pelycosauria. Geol. Soc. Amer. Spec. Pap. No. 28, 538 pp.

MUS. COMP. ZOOL
LIBRARY
MAR 18 1985
HARVARD
UNIVERSITY

B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 29 APRIL 1983 NUMBER 475

NEW OR PROBLEMATIC *ANOLIS* FROM COLOMBIA. I. *ANOLIS CALIMAE*, NEW SPECIES, FROM THE CLOUD FOREST OF WESTERN COLOMBIA

STEPHEN AYALA,[1] DENNIS HARRIS,[2] AND ERNEST E. WILLIAMS[3]

ABSTRACT. *Anolis calimae*, new species, is described from the cloud forest of western Colombia in Departmento Valle del Cauca. Referable to the *Anolis punctatus* species group, it is distinctive in its coloration, in the absence of an interparietal scale, and in the apparent trend to reduction of the elongate anterior supraciliary scale usual in *Anolis*.

INTRODUCTION

In a recent paper (Williams, 1982), the description of three new species was made the occasion of a summary of the eastern members of the *punctatus* species group. Several new species must be described before a similar summary will be possible for the western *punctatus* group. The first is here described, a small species and initially recognized only from a single specimen collected in cloud forest near Lake Calima. Even with one specimen, its striking color pattern and distinctive habitus made it obvious that it is a new species. Subsequently, three additional specimens have been obtained, one from the original locality, two from Television Tower Mountain near Cali. These four specimens have been divided between the Museum of Comparative

[1]120 Vista View Place, Petaluma, California 94952.
[2]Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109.
[3]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

Zoology and the Instituto de Ciencias Naturales (ICN, Bogotá). Still more recently a Museo La Salle (MLS, Bogotá) specimen from a third locality has been recognized as belonging to this species. At the suggestion of Fernando Castro, we call it after the place of its first discovery:

Anolis calimae, new species
(Figs. 1–6)

Type: MCZ 158392, adult male.

Type locality: San Antonio, Television Tower Mountain, Depto. Valle del Cauca, Colombia, (3° 28′N 76° 40′ W) 1,800 m elevation, Dennis Harris, Humberto and Fanny Carvajal, coll., 23 January 1980.

Paratypes (all from Valle): MCZ 158393, adult female, same data as type; ICN 3678, adult female, approx. 1 km below Lake Calima dam, (3° 50′N 76° 32′W) Dennis Harris, coll., 18 January 1980; ICN 3679, adult male, same place as ICN 3678, William Duellman and Fernando Castro, coll., 17 March 1979. MLS 122: Mares, 3 km N of San Antonio (3° 30′N 76° 40′W).

Diagnosis. A small green cloud forest species of the *punctatus* group distinguished by its short body, legs and tail, *consistent absence of the interparietal scale*, a blunt and weak canthal ridge with poorly differentiated canthal scales, only a short supraciliary scale followed by granules or granules only, small, low number of loreal scales (4–5), smooth ventrals and very short stubby toes with 15 to 17 lamellae under phalanges ii and iii of fourth toe. Dewlap present in both sexes, small in female and *with larger scales*.

Description. Head. Rather short. Head scales small, flat, very slightly wrinkled. Seven to ten scales across the snout between the second canthals. Frontal depression shallow, the scales within it as large or larger than some of those anterior to it. Four to seven scales border rostral posteriorly. Circumnasal scales of each side separated from rostral by one elliptical scale which lies above the suture between rostral and first supralabial. Six scales between supranasals dorsally. Snout elongate, slightly protuberant, extending slightly beyond mental.

Supraorbital semicircles separated in both males by two rows of large scales, as large as the scales of the semicircles, in the females in contact or separated by one row of small scales or granules. Supraor-

Figure 1. *Anolis calimae*, new species, in life. Female paratype above, male type below.

bital scales in contact with or barely separated from the supraocular disk of each side, which consists of six to ten enlarged, slightly wrinkled scales, remainder of the supraocular area granular or subgranular. One or two short supraciliaries on each side followed by granules, or *only granules present*. Canthus blunt, canthals small, poorly differentiated, the first or first and second largest. Loreal rows four or five, the lowermost slightly larger.

Temporals granular. An indistinct intertemporal double line of slightly enlarged scales. Supratemporals granular laterally, becoming larger and flattened toward the interparietal area, which is bounded by weak ridges. *No differentiated interparietal*, but a zone of enlarged scales, largest anteriorly and laterally, posteriorly grading slowly into the dorsal granules. Ear opening small, elliptical, but larger than any scale in the interparietal area. Occiput with small blunt median knob, obvious in males, not evident in females.

Suboculars in contact with supralabials. Seven supralabials to the center of the eye.

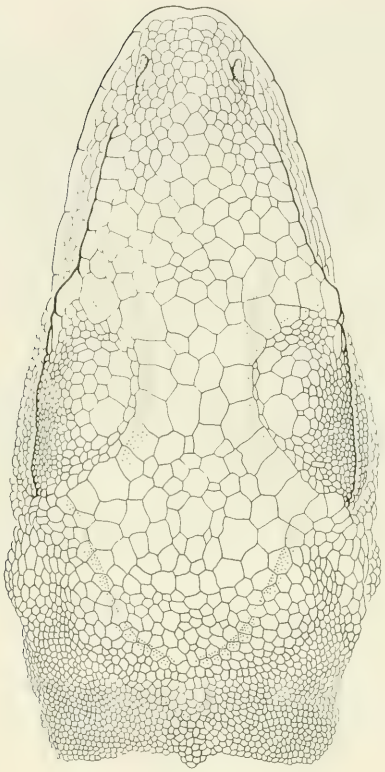


Figure 2. *Anolis calimae*, new species. Male type, MCZ 158392. Dorsal view of head.

Mental semidivided, each part slightly or distinctly wider than deep. Four granules are in contact with the mental between the large first sublabials. Two to five sublabials in contact with the infralabials. Gular scales subgranular, very little enlarged laterally where they border the sublabials.

Trunk. Dorsal scales granular, convex, subequal. Ventrals much larger, smooth, juxtaposed or subimbricate, rounded or slightly pointed in males, broader, squarish in females, in tranverse rows. Lateral chest scales not keeled. Males may develop a low nuchal crest when aroused.

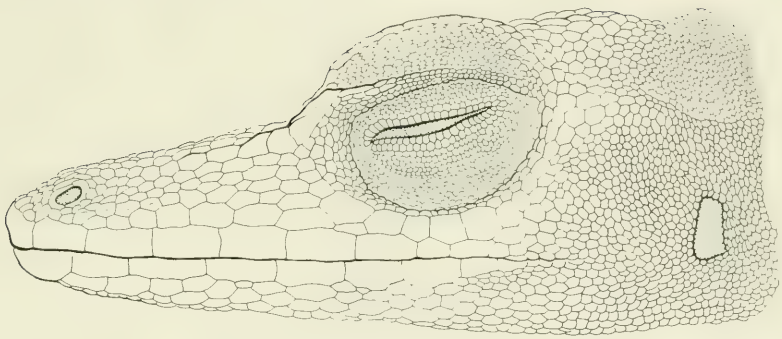


Figure 3. *Anolis calimae*, new species. Male type, MCZ 158392. Lateral view of head.

Dewlap. Present in both sexes. Large in male, reaching anterior abdomen, scales small, smaller than ventrals, weak, in rows, one scale wide, separated by naked skin, edge scales larger, somewhat crowded, imbricate, smooth; small to moderate in females, *scales larger*, as large or larger than ventrals, in close-packed rows, smaller and much more numerous along the edge.

Limbs and digits. Upper arm scales granular. Lower arm scales granular to larger and unicarinate. Leg scales granular posteriorly, larger and uni- to multicarinate anteriorly. All supradigital scales multicarinate. Toes relatively short and stubby. Digital dilations moderately wide. Fifteen to 18 scales under phalanges ii and iii of fourth toe.

Tail. Compressed, short, ca. 1.5 X body length, possibly prehensile. No tail crest. Two weakly keeled middorsal rows, ventral rows larger and more strongly keeled, verticils not evident. Scales posterior to vent smooth. Large postanals in males, none in females. Tail base prominently swollen to accommodate hemipenes in adult males.

Size. *Anolis calimae* is a small but somewhat robust species. Sizes of the four recent specimens are: 59 (type), 58, 55, and 58 mm snout-vent length respectively.

Color. This is a green anole with a considerable capacity for rapid pattern and color change. It may be almost uniform green or yellow-green with little or no pattern, or it can have three prominent broad

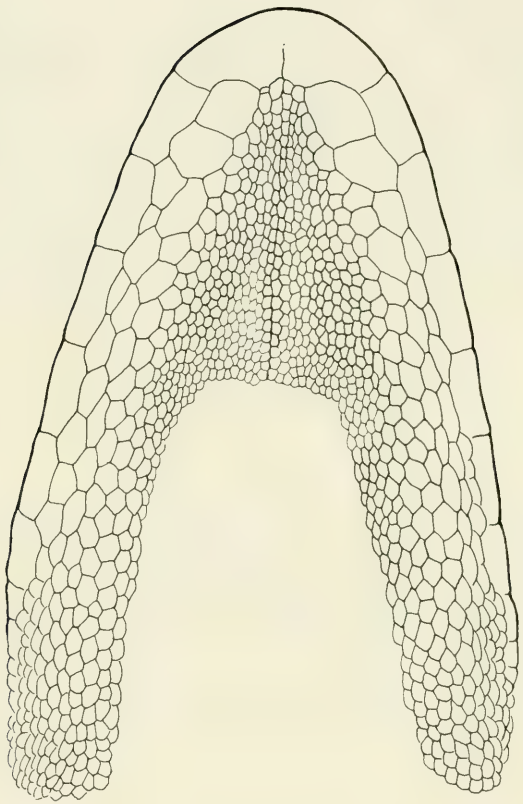


Figure 4. *Anolis calimae*, new species. Male type, MCZ 158392. Ventral view of head.

black bands across the back and sides (apparently more prominent in the males), with pale yellow or cream colored spots in the dark bands. At another state of excitement, the sides and back are mostly green-grey with scattered small black spots on the sides and neck and a few dark brown crossbars on the vertebral line. Females especially may show alternating sets of narrow, light yellow and dark brown-black spots along the midline. There is no prominent dark band across the head between the eyes. The large male dewlap is unpigmented: pale yellow-green with salmon pink near anterior edge and white or pale

Figure 5. *Anolis calimae*, new species. Male type in lateral view.

yellow scales. The small female dewlap is pigmented: blue with yellow or white scales. The tail is banded: broad dark bands in the male and narrow bands in the female. The lining of the throat is pale. The iris of ICN 3678 (a female) was golden yellow above and below a zone of orange; that of the holotype male, MCZ 158392, was orange.

Preserved specimens are greenish-grey with few to many small but prominent dark (and light in the male) spots on the back and sides, elongate dark and light spots along the dorsal midline and a darker brown, unpatterned head. The belly is pale, with small grey spots under the chin. The dewlap has rows of white scales over white skin (males) or pigmented skin (females). The peritoneal lining is heavily pigmented.

Habitat and reproduction. The two recent collection sites are about 50 km apart in the same cloud forest region (tropical premontane wet forest) in the western Colombian cordillera. All four specimens were collected at night while they were sleeping in exposed sites 40 to 150 cm above the ground, the type and first paratype on a fern leaf and a low shrub, in a cool forested region at about 1,800 m elevation. The two Lake Calima paratypes were on exposed twigs, in a somewhat warmer, more densely vegetated area also subject to frequent rains and cool fogs at 1,300 m elevation. Other anoline species known to occur in the same sites or in the same general area are *A. ventrimaculatus, A. eulaemus, A. fraseri, A. antonii, Phenacosaurus heterodermus* and an undescribed *punctatus* group anole known at present from a single specimen.

The specimens were in reproductive condition at the time of capture: the males with enlarged testes (6.1 x 4.0 mm approx.), and the females with a single oviducal egg on one side and an enlarged, yolking follicle on the other.

Etymology. The name *calimae* refers to the site where William Duellman and Fernando Castro collected the first specimen. Lake Calima is in turn named after the Calima Indians who inhabited the region centuries ago.

Comparisons. A. calimae is a very distinctive anole. No previously described member of the *punctatus* group is known to lack an interparietal scale. This condition is unusual in any group of *Anolis*, but it is curious that it is known as a moderately common variation in two species of the *aequatorialis* species group (*A. ventrimaculatus* and *A. gemmosus*) which, like *calimae*, are inhabitants of Andean cloud

Figure 6. *Anolis calimae*, new species. Female paratype in lateral view.

forest. It is possible, since there are only four specimens of *calimae* thus far known, that absence of an interparietal will be found to be inconstant in this species too.

The wholly granular supraciliary margin found in one specimen of *calimae* is unique, not only for the *puncatatus* group, but for the genus *Anolis*. The alternative and commoner condition (in three of the four *calimae*) of one elongate but short supraciliary scale is known elsewhere (e.g., in the *tigrinus* species group); the extreme shortness of the scale in the three specimens may, however, be indicative of a strong trend toward de-differentiation of this scale, which then culminates in the completely granular margin.

The presence of a dewlap in both sexes, and the fact that it is smaller and differently pigmented in the female, may be a primitive feature of *calimae* and occurs erratically in a number of *Anolis* species groups. In the *punctatus* group the condition is known in *chocorum* and in *transversalis*, and in these species, as in *calimae*, is associated with a more or less marked difference in body color and pattern between the sexes.

Unique to *calimae* is the larger size of the dewlap scales in the female. The reverse or equal-sized scales is typical for *Anolis* species in which the female retains a dewlap.

Unusual also and requiring confirmation by additional material is the apparent difference between males and females of *calimae* in the size and number of scales between the supraorbital semicircles.

From the two other previously described *punctatus* group species of western Colombia *A. calimae* is as distinctive in color as in scales. Both these species are also Pacific lowland forms: *Anolis chocorum* (also a larger species, reaching 79 mm snout-vent length) has the dorsum uniform green or with oblique rows of dark green blotches on the flanks, never with prominent black bands enclosing yellow or cream spots. The male dewlap is orange laterally, green basally; or the female dewlap is green with pale yellow or gray at the base. The rows of scales in the dewlaps are three to four scales wide. *Anolis chloris* (about the same size as *A. calimae*, ca. 55 mm snout-vent length) is grass-green in color, with the potentiality of turning a dark olive green which then may have diagonal darker bars, but again there are never the black bands of *calimae*. The dewlap color in males is yellow or white, never green, the rows of scales in the dewlap are one scale wide and there is no dewlap in the female. In contrast to *A. calimae*, both *A. chocorum* and *A. chloris* turn blue or purple in preservative

rather than the greyish green of *A. calimae*. The occiput knob is not seen in *A. chocorum* or *A. chloris*.

There has been no evident close relative for *A. calimae*. However, an undescribed species from the same region, known only from a juvenile male, seems closer than any other, although still sharply distinct.

ACKNOWLEDGMENTS

We are grateful to the collectors of the species here described, William E. Duellman, Humberto and Fanny Carvajal, and Fernando Castro. Ayala's work in Colombia was sponsored by grants from the U.S. Public Health Service (NIAID AI-A21511), Tulane University (NIAID AI-10050), and COLCIENCIAS, the Colombia National Science Institute. The drawings are by Laszlo Meszoly.

LITERATURE CITED

Williams, E.E. 1982. Three new species of the *Anolis punctatus* complex from Amazonian and inter-Andean Colombia, with comments on the eastern members of the *punctatus* group. Breviora Mus. Comp. Zool. No. 467, pp. 1–38.

MUS. COMP. ZOOL.
LIBRARY
MAR 1 8 1985
HARVARD
UNIVERSITY

BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 29 APRIL 1983 NUMBER 476

TOWNSEND'S UNMAPPED NORTH ATLANTIC RIGHT WHALES *(EUBALAENA GLACIALIS)*

WILLIAM E. SCHEVILL[1] AND KAREN E. MOORE[2]

ABSTRACT. Townsend's detailed maps of worldwide whale distribution from 19th century American whaling logbooks (1935, Zoologica, N.Y., **19:** 1–50) omitted his North Atlantic records for *Eubalaena.* We have read 12 of his 15 sources and have mapped the right whales therein recorded.

INTRODUCTION

Very little is known about the distribution of right whales *(Eubalaena glacialis)* in the North Atlantic Ocean. Among others, J. A. Allen (1908), Collett (1909), G. M. Allen (1916), Thompson (1928), Slijper, van Utrecht, and Naaktgeboren (1974), Reeves, Mead, and Katona (1978), Schevill, Moore, and Watkins (1981), Kraus and Prescott (1981), Reeves and Brownell (1982), and Watkins and Schevill (in press) have discussed sightings and catches in particular areas. Townsend (1935), in his study of "the distribution of certain whales as shown by logbook records of American whaleships," examined logbooks from 1,665 voyages, worldwide, mostly of the 19th century. Out of the 8,415 *Eubalaena* taken, he found only 35 in the North Atlantic, recorded on 15 voyages, and did not bother to plot these on his charts by latitude, longitude, and month as he did the rest of his total of 53,877 whales of six species (see his pp. 10 and 18). Our note is a response to this omission, and like Townsend's paper is based only

[1]Museum of Comparative Zoology, Cambridge, MA 02138 and Woods Hole Oceanographic Institution, Woods Hole, MA 02543.
[2]Woods Hole Oceanographic Institution, Woods Hole, MA 02543.

on Yankee whaling logbooks. Thus it does not deal with the historic *Eubalaena* fishery of the eastern North Atlantic, well-established in the Bay of Biscay by the 12th century, and continuing intermittently along the western coast of Europe from the Mediterranean to the Barents Sea (where this whale got the name of nordkaper) and Iceland; this fishery pretty well stopped in the 1920's, and now *Eubalaena* is very rarely seen in those waters.

Because so little is known, the location and season of even Townsend's few North Atlantic right whales are important. We have consulted 12 of his 15 sources (Table 1), but failed to find the other three logbooks, which he credits with one North Atlantic right whale each (sloop GREYHOUND, 1753; ship GOVERNOR TROUP, 1868–70; bark SEA RANGER, 1879–84). The Providence Public Library has a partial journal by William H. Tilton, a boatsteerer/third mate of SEA RANGER during this voyage, but it does not tell where whales were encountered. The 12 logbooks that we read are listed by Townsend as recording the other 32 *Eubalaena glacialis*.

Our results do not entirely agree with Townsend's. For one thing, as he explains on page 16, his counts of whales include "not only the whales turned into oil ['saved', as the whalers said], but also those killed... but subsequently lost." In our logbook reading we have tried to separate these categories, and since we are interested more in whale distribution than in oil production, we have also counted whales sighted (and identified) but not struck. The logs do not always specify the numbers sighted if greater than 1 or 2. When they said merely "right whales," we counted it as 2+; the sum of 5+ and 4+ is given conservatively as 9+, though the actual count might have been appreciably higher. We assume that these old-time whalers were competent at recognizing the species of interest —probably much more reliably than most seafarers of today; sometimes sightings were logged simply as "whales," and these we did not count. We cannot explain our discrepancies with Townsend, and can only say that we have reported what we found in our reading. We failed to find mention of the single *Eubalaena* each that he recorded for JIREH SWIFT and EMMA JANE, and of the 3 he ascribed to ENDEAVOR.

Table 1. Reexamination of Townsend's original sources for North Atlantic right whales, with location of these logbooks. The first five columns are our findings, and the last column is from Townsend.

Voyage	Saved	Struck and Lost	Sighted	Total	Location	Townsend 1935
GREYHOUND, sloop, 1753		Logbook not found				1
JIREH SWIFT, ship, 1853-55, N.B.P.L.	0	0	0	0		1
ENDEAVOR, bark, 1854-56, N.B.P.L.	0	0	0	0		3
RICHMOND, bark, 1857-60, O.D.H.S.	8	0	1	9	Cintra Bay	9
ANSEL GIBBS, bark, 1868-69, O.D.H.S.	1	1	0	2	Denmark Str.	2
GOVERNOR TROUP, ship, 1868-70		Logbook not found				1
GOLDEN CITY, schr., 1875-76, P.P.L.	1	0	0	1	Fernandina, Florida	1
A. J. ROSS, brig, 1877, O.D.H.S.	4	0	7+	11+	7+ Denmark Str. 4 Cintra Bay	4
DANIEL WEBSTER, ship (bk.), 1877-79, P.P.L.	1	4	1	6	2 Denmark Str. 3 49° N, 23° W 1 50° N, 23° W	1
EMMA JANE, schr., 1879-80, O.D.H.S.	0	0	0	0		1
SEA RANGER, bark, 1879-84		Logbook not found				1
A. R. TUCKER, bark, 1880-83, N.B.P.L.	1	1	4	6	Denmark Str.	1
GOLDEN CITY, schr., 1881-82, O.D.H.S.	1	0	0	1	Georgia, U.S.A.	1
PALMETTO, bark, 1886, O.D.H.S.	5	2	8+	15+	Denmark Str.	5
CANTON, bark, 1897-98, N.B.P.L.	0	2	3	5	3 Denmark Str. 2 47° N, 43° W	3
	22	10	24+	56+		35

N.B.P.L. = New Bedford Public Library
O.D.H.S. = Old Dartmouth Historical Society
P.P.L. = Providence Public Library

FINDINGS

The 12 voyages summarized (Table 1) for *Eubalaena glacialis* in the North Atlantic were made by 11 whaleships over a 45-year span (1853 to 1898). The highest and lowest latitudes reached by these are well within the known range of this species. No *Eubalaena* were recorded in the months of January, April, September, October, and December. The records from November through March are all south of N. lat. 32°, and those from May through August are between N. lat. 46° and 62°, but there is no detailed evidence for migration patterns. We find the whales in high latitudes in summer and lower in winter, but there are no helpful hints of routes to and fro. The winter records are right along the shore on both sides of the Atlantic (Cintra Bay, N. lat. 23° in western Africa, and N. lat. 31° at the Georgia-Florida border in North America); on each coast the ship sometimes anchored and whaled from the boats.

Six voyages (ANSEL GIBBS in 1868, DANIEL WEBSTER and A. J. ROSS in 1877, A. R. TUCKER in 1880, PALMETTO in 1886, and CANTON in 1897) reported whales in June, July, and August to the eastward of Cape Farewell, Greenland, between N. lat. 59° and 62°, W. long. 32° and 38°, at the southern entrance to Denmark Strait. They logged 12 whales saved, 7 struck but lost, and at least 16 more sighted; Townsend recorded 16 whales, but without specifying the region (3 of these voyages whaled also in other areas). These 35 whales were encountered in 26 ship-weeks of hunting in five years, which implies a consistently good hunting ground. This ground is not referred to by name in these logs. We found no hint that bowheads were seen or taken, although they might have been expected in these waters. (For a recent report, see Jonsgård, 1982, Fig. 1.) As pointed out by J. A. Allen (1908: 281–288 and especially 286), since the 17th century whalers have distinguished bowhead (*Balaena mysticetus*) from nordkaper, or right whale in American usage (*Eubalaena glacialis*), both on morphology and oil yield, as well as on behavior. While the Ross was on these Denmark Strait grounds near N. lat. 60° and W. long. 35°, the whales were specified as "Wright Whales" and seven or more were sighted, of which four were saved. After leaving these grounds, the Ross went through the Canaries, and on 24 November "Saw A Wright Whale" in "Senter Bay" (Cintra Bay) on the African coast. Therefore we conclude that only *Eubalaena glacialis* were found on these voyages.

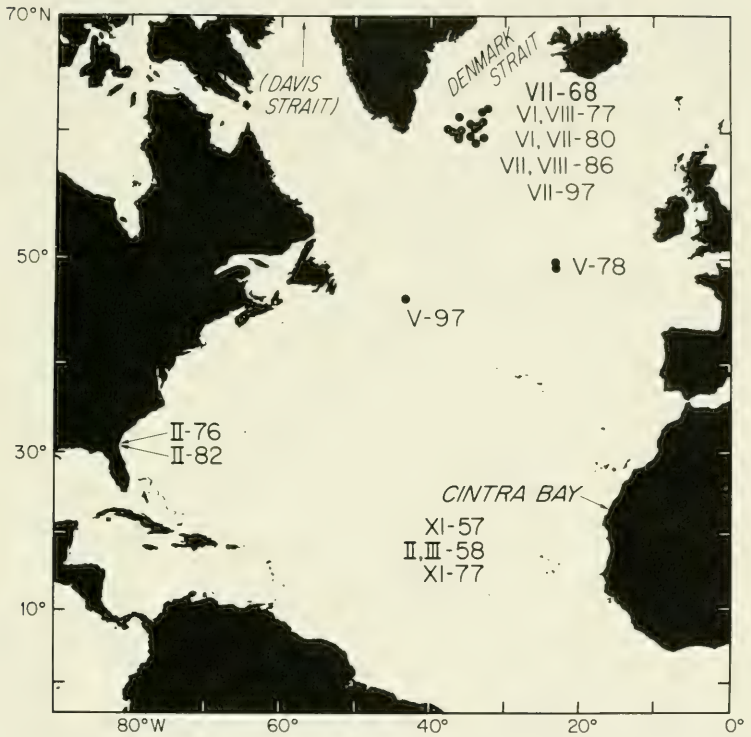


Figure 1. Distribution of North Atlantic right whales *(Eubalaena glacialis)* recorded in American whaling logbooks between 1857 and 1897. The dots show where whales were encountered at sea, and the coastal encounters are indicated by arrows. Months are indicated by roman numerals.

Although these whaleships departed and returned to port (usually New Bedford) in all seasons, there is no mention of right whales seen near the New England or Canadian coasts. Before the mid 1700's right whales were caught in Massachusetts waters from small shore-based boats, mostly in the winter and spring (Macy, 1835). From 1955 to the present, right whales have been observed locally in all seasons (Schevill, Moore, and Watkins, 1981; Watkins and Schevill, in press). It seems highly unlikely that these 19th century whalers would have ignored such valuable animals wherever seen, and so it may be that *Eubalaena* were then very scarce in these coastal waters, although they had been abundant there from the 16th well into the 18th centuries.

Against the background of scanty and often imprecise data on the seasonal and geographic distribution of *Eubalaena glacialis,* even these few additional points are significant. We have mapped about 60 whales logged on 9 voyages by 8 ships during the 40 years from 1857 to 1897. More than half of these were in the Denmark Strait area in June, July, and August. More than 13 of the remainder were at Cintra Bay in November, February, and March.

A question about the North Atlantic *Eubalaena* has been whether there was more than one stock in the population. Did the relative abundance that we report for Denmark Strait a hundred years ago hint that right whales from both sides of the North Atlantic summered together, indicating one general population for this ocean? Or might there have been two stocks, with Cintra Bay perhaps being in the winter range of the nordkapers of the Barents Sea? This is the sort of problem for which radio tagging and tracking are needed. There are still at least several hundred *Eubalaena* in the North Atlantic.

ACKNOWLEDGMENTS

We would like to acknowledge help from Stuart C. Sherman, who told us where to find the logbooks, Richard Kugler and Virginia Adams of the Old Dartmouth Historical Society, Paul Cyr of the New Bedford Public Library, and Lance Bauer of the Providence Public Library; Colleen Hurter helped with bibliothecal matters. William A. Watkins and Richard H. Backus helpfully commented on the manuscript. Support for this study was from the Oceanic Biology Program of the Office of Naval Research, Contract No. N00014-82-C0019 NR083-004. This is Contribution No. 5241 from the Woods Hole Oceanographic Institution.

LITERATURE CITED

ALLEN, G. M. 1916. The whalebone whales of New England. Mem. Boston Soc. Nat. Hist. **8**(2):107–322, plates 8–16.

ALLEN, J. A. 1908. The North Atlantic right whale and its near allies. Bull. Am. Mus. Nat. Hist., **24**: 277–329, plates 19–24.

COLLETT, R. 1909. A few notes on the whale *Balaena glacialis* and its capture in recent years in the North Atlantic by Norwegian whalers. Proc. Zool. Soc. Lond., 1909: 91–98, plates 25–27.

JONSGÅRD, Å. 1982. Bowhead (*Balaena mysticetus*) surveys in the Arctic Northeast Atlantic waters in 1980. Rep. Int. Whal. Commn., **32:** 355–356.

KRAUS, S. D., and J. H. PRESCOTT. 1981. Distribution, abundance and notes on the large cetaceans of the Bay of Fundy, summer and fall 1980. Final Report to the U.S. Department of Commerce, NOAA, National Marine Fisheries Service, 87 pp.

MACY, O. 1835. The History of Nantucket. Hilliard, Gray, and Co., Boston, 300 pp. Reprinted by Research Reprints Inc., New York, 1970.

REEVES, R. R. AND R. L. BROWNELL, JR. 1982. Baleen whales. *Eubalaena glacialis* and allies, pp. 415–444. *In* J. Chapman, G. Feldhamer (eds.), *Wild Mammals of North America.* The Johns Hopkins University Press.

REEVES, R. R., J. G. MEAD, and S. KATONA. 1978. The right whale, *Eubalaena glacialis,* in the western North Atlantic. Rep. Int. Whaling Comm., **28:** 303–312.

SCHEVILL, W. E., K. E. MOORE, AND W. A. WATKINS. 1981. Right whale, *Eubalaena glacialis,* sightings in Cape Cod waters. Ref. No. 81–50, Woods Hole Oceanographic Institution, 16 pp.

SLIJPER, E. J., W. L. VAN UTRECHT, and C. NAAKTGEBOREN. 1964. Remarks on the distribution and migration of whales, based on observations from Netherlands ships. Bijdragen tot de Dierkunde, Aflevering **34**: 3–93.

THOMPSON, D'ARCY W. 1928. On whales landed at the Scottish whaling stations during the years 1908–1914 and 1920–1927. Fishery Board Scotl., Sci. Invest. 3, 39 pp.

TOWNSEND, C. H. 1935. The distribution of certain whales as shown by logbook records of American whaleships. Zoologica, **19** (1): 1–50, plates 1–4.

WATKINS, W. A., AND W. E. SCHEVILL. In press. Observations of right whales (*Eubalaena glacialis*) in Cape Cod waters. Fishery Bull.

POSTSCRIPT

While this paper was in press, we were enabled by the courtesy of Professor Howard E. Winn of the University of Rhode Island to consult a collection of about half the worksheets used in preparing the maps of Townsend's 1935 compilation. These had been preserved at the New York Zoological Society; for each logbook they tally the date, location, and species of each whale taken. The logbooks are of course the primary sources, but these tallies tell us something of the compilation, and account for occasional discrepancies. Thus we have learned that the particular EMMA JANE logbook read by us is incomplete; it ends on 1 January 1880. The tally shows that the voyage continued into August 1881, and that this schooner did take a right whale on 15 February 1880 off Brunswick, Georgia, near where GOLDEN CITY took her 2 whales of 1876 and 1882, also in the latter part of February. The tally for ENDEAVOR 1854–1856 confirms our failure to find in her logbook any right whale captures during either North Atlantic passage, and shows that

the 3 whales published as from that ocean were actually taken in the Sea of Okhotsk. The GOVERNOR TROUP tally for 1868–1870 tells us that the whale listed for the North Atlantic was taken in the South Atlantic, 20 miles east of Tristan da Cunha in about 37° 15′S. We still have not seen her actual logbook. The CANTON tally for 1897–1898 counts 1 of the 2 whales that we list as struck and lost in July; the other 2 cited as North Atlantic turn out to have been taken in the South Atlantic in November. The sheets for JIREH SWIFT are missing, as are those for SEA RANGER and the sloop GREYHOUND; we hope that someone will find our three missing logbooks.

MUS. COMP. ZOOL.
LIBRARY
MAR 18 1985
HARVARD
UNIVERSITY

BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 7 SEPTEMBER 1984 NUMBER 477

NEW OR PROBLEMATIC *ANOLIS* FROM COLOMBIA. II. *ANOLIS PROPINQUUS*, ANOTHER NEW SPECIES FROM THE CLOUD FOREST OF WESTERN COLOMBIA.

ERNEST E. WILLIAMS[1]

ABSTRACT. *A. propinquus*, new species, from the cloud forest of Departamento Valle in western Colombia resembles sympatric *A. calimae* Ayala, Harris, and Williams in the absence of an interparietal scale, but differs by its uniform coloration, distinctly keeled head scales, elongate supraciliary scales, and blue rather than yellow dewlap.

Another western *punctatus* group species has languished unrecognized in the Museum of Natural History, the University of Kansas (KU), since its collection in 1974. Known only from a male near hatchling, it is unremarkable as regards color, but it is structurally nearly as distinctive an animal as the recently described *A. calimae* with which it occurs.

Because it is another member of an anole fauna that is just beginning to be known, it receives the Latin name that means 'neighbor':

Anolis propinquus, new species
(Figs. 1–3)

Type: KU 169833, male juvenile.

Type locality: Río Calima, 1.5 km W Lago Calima, Valle, Colombia, W. E. Duellman, coll., 15 September 1974.

Diagnosis. Another green cloud forest species of the *punctatus* group somewhat similar to *A. calimae* and, like that species, lacks a

[1]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

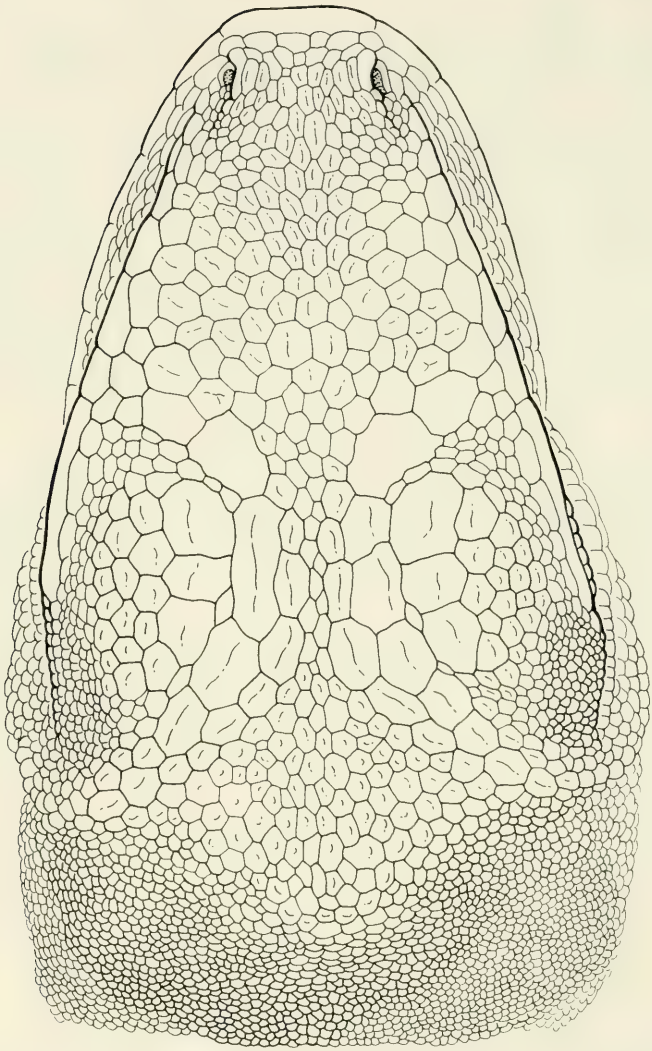


Figure 1. *Anolis propinquus,* new species. Holotype, KU 169833. Dorsal view of head.

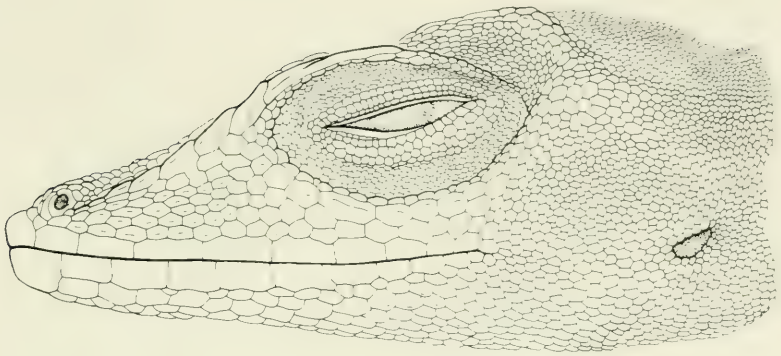


Figure 2. *Anolis propinquus*, new species. Holotype, KU 169833. Lateral view of head.

parietal eye, but distinguished among other features by keeled head scales, an elongate supraciliary scale which occupies half the supraciliary margin, a higher number of loreal rows (7) and a higher lamellar count under phalanges ii and iii of the fourth toe (25), and its blue rather than yellow dewlap.

Description. Head. Blunt, short. Head scales rather small, most scales unicarinate, the keels irregular in direction. Twelve scales across snout between second canthals. Frontal depression very shallow, the scales within it larger than those anterior to it. Six scales border rostral posteriorly. Anterior nasal scale weakly differentiated, narrow, separated from the rostral-first supralabial suture by one scale. Eight scales between supranasals dorsally.

Supraorbital semicircles separated by three rows of scales, the lateral ones almost as large as the scales of the semicircles and keeled, the middle row minute, granular. Supraocular disk moderately developed, containing ca. 21 keeled scales, those next to the semicircles largest, grading laterally into smaller but still keeled scales, two rows of subgranular scales separating the disk on each side from the supraciliaries. Anterolateral corner of supraocular area with subgranular scales, posterolateral corner with minute granular scales. One elongate supraciliary *extending half the supraciliary distance* and followed by granules. Canthus blunt, of ca. seven scales, the first, second and third larger. Seven loreal rows below second canthal.

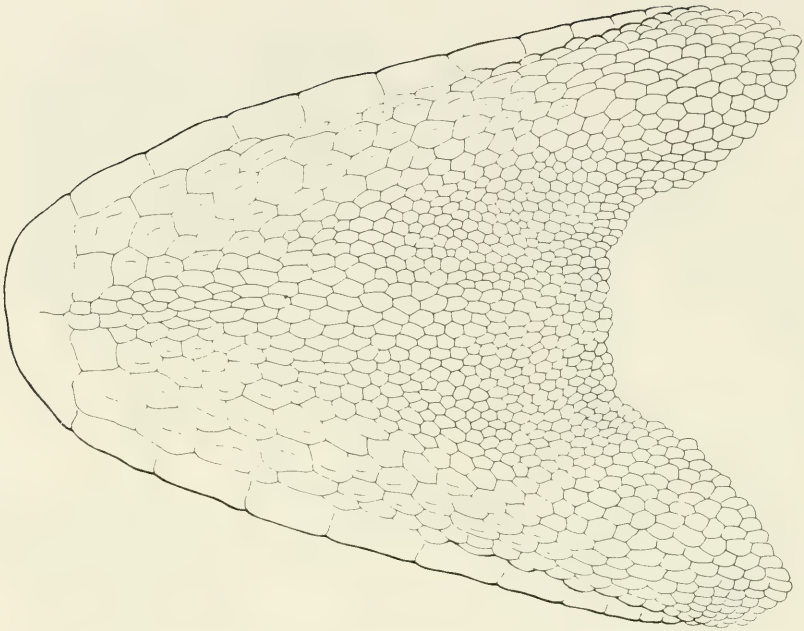


Figure 3. *Anolis propinquus,* new species. Holotype, KU 169833. Ventral view of head.

Temporal scales granular, a triangle of subgranular intertemporal scales. Supratemporal scales granular, minute, becoming abruptly larger toward the interparietal area. Ear small, but larger than any presumptive interparietal. Enlarged scales of interparietal area largest laterally, all abruptly larger than the minute nape scales which are distinctly smaller than the dorsals. No parietal eye.

Suboculars weakly keeled, separated from the supralabials by one row of scales. Seven to eight supralabials to the center of the eye.

Mental divided, each half a little wider than long. Two small scales posteriorly in the notch between the mentals. Two much larger rectangular scales lateral to them, between the trapezoidal first sublabials. Three sublabials in contact with the infralabials on each side.

Throat scales swollen, rather elongate, minute posteriorly, becoming larger anteriorly and laterally.

Trunk. Dorsal scales granular, convex, subequal. Ventrals not much larger, swollen, smooth, juxtaposed or subimbricate, in transverse rows. *An umbilical scar still detectable.*

Dewlap. Retracted in the unique type, not readily visible. Large, scales crowded, swollen, imbricate, raised into series of rows or ridges, a little smaller than the ventrals.

Limbs and Digits. Anterior arm and leg scales unicarinate except multicarinate at the knee. Supradigital scales multicarinate. Ca. 25 lamellae under phalanges ii and iii of fourth toe.

Tail. Weakly compressed. No dorsal crest. One row of keeled scales middorsally, not differentiated from those lateral to it. No evident verticils. Enlarged postanals present (♂).

Size. The snout-vent length of the unique type is 41 mm.

Color. As preserved, the specimen shows no pattern: it is dark above, light below and the dewlap skin appears to be dark. W. E. Duellman provides notes of color in life: "Dorsum green. Venter pale bluish green. Dewlap pale blue. Iris dark brown. Mouth bluish black, tongue pink."

Habitat. The only notes on habitat or ecology are Duellman's: "Sleeping on herb ca. 0.5 m above ground at night."

Comparisons. The most pertinent comparison of *A. propinquus* is with sympatric and just-described *A. calimae* (Ayala *et al.*, 1983) (Table 1). The unique type is a near hatchling, but the dewlap is already well indicated, extending posterior to the axilla and the high number of lamellae under the fourth toe (25) indicates a species of at least moderate size.

It is again astonishing to find the interparietal reduced (i.e., a parietal eye lacking). In contrast to *A. calimae,* the supraciliary scales are unusually well developed and the head scales very distinctly keeled. The blue dewlap is also distinctive.

ACKNOWLEDGMENTS

I am grateful to William E. Duellman, Curator at the Museum of Natural History, University of Kansas for the opportunity to examine and describe this peculiar animal. The drawings are by Laszlo Meszoly.

Table 1. **Comparison of *Anolis calimae* and *A. propinquus*.**

	calimae	*propinquus*
scales across snout	wrinkled	unicarinate
number between second canthals	7–10	12
circumnasal/rostral scale	separated by one round scale	a weakly differentiated subtriangular anterior nasal scale
scales between supraorbital semicircles	2 large squarish scales in males, none or one row of small scales in females	3 rows of scales, the lateral ones large and keeled, the middle minute
scales of supraocular disk	smooth or wrinkled	keeled
differentiated supraciliaries	one short or *none*	one very elongate (½ supraciliary margin)
loreal rows	4–5	7
interparietal	not differentiated	not differentiated
scales between interparietal and semicircles	not determinable	not determinable
scales between supraoculars and supralabials	0	1
supralabials to center of eye	7	7
trunk scales	uniform, granular	uniform, granular
ventrals	larger than dorsals, smooth, juxtaposed or subimbricate	larger than dorsals, smooth, juxtaposed or subimbricate
dewlap	large in ♂, smaller in ♀	large in *juvenile* male
dewlap scales	lateral scales smaller in males than in females, smaller than ventrals	only male known
dewlap skin	unpigmented in ♂, pigmented in ♀	pigmented in ♂
postanal scales	very large in ♂, absent in ♀	large in ♂

Table 1. **Comparison of *Anolis calimae* and *A. propinquus*.**

	calimae	*propinquus*
scales posterior to vent	smooth	smooth
tail	compressed	slightly compressed
tail crest	not a crest, but *2* middorsal rows	not a crest but a *single* middorsal row

LITERATURE CITED

Ayala, S., D. Harris, and E. E. Williams. 1983. New or problematic *Anolis* from Colombia. 1. *Anolis calimae*, new species from the cloud forest of western Colombia. Breviora Mus. Comp. Zool., No. 475, pp. 1–11.

MUS. COMP. ZOOL.
LIBRARY
MAR 18 1985
HARVARD
UNIVERSITY

BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 7 SEPTEMBER 1984 NUMBER 478

NEW OR PROBLEMATIC *ANOLIS* FROM COLOMBIA. III. TWO NEW SEMIAQUATIC ANOLES FROM ANTIOQUIA AND CHOCÓ, COLOMBIA.

ERNEST E. WILLIAMS[1]

ABSTRACT. Two new semiaquatic anoles from Colombia, partly sympatric, and sometimes syntopic, prove to belong to distinct lineages despite convergence in habits and habitat. The larger of the two—*A. maculigula,* new species—belongs to the alpha section of the genus *Anolis* and the *eulaemus* subgroup of the *A. aequatorialis* species group. It is confined, so far as known, to the Departamento Antioquia and apparently to larger streams. The smaller species, *A. rivalis,* new species, is a beta anole of the *lionotus* species group and tends to prefer smaller streams and extends beyond the known range of *A. maculigula* in Antioquia and in Chocó.

In 1968 Norman J. Scott, collecting on a tributary of the Río Arquía in western Antioquia, Colombia, obtained a large anole of aquatic habits which he thought resembled *A. aquaticus.* It proves, however, to be a new species belonging to the alpha section of the genus. Syntopic with this species was a smaller form which Scott recognized as a member of the *lionotus* species group (beta section). This also proves to be new. These specimens were deposited in the collections of the Los Angeles County Museum (LACM).

Since these first collections, additional material of both species has been obtained in another area of western Antioquia some 70 km farther north by Juan Manuel Renjifo and Vladimir Corredor (material in the Instituto de Ciencias Naturales, Bogota [ICN]). Specimens of the larger species have been collected at Urrao, Parque Las Orquídeas, ca. 50 to 60 km east of the type locality, by

[1]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

Horatio Echeverri for Marco Serna (collection of Colegio San José, Medellin (CSJ). Specimens of the smaller species have been collected in the Chocó independently by Philip Silverstone (MCZ) and Charles Myers (ICN). A further Chocó specimen of the smaller species has been found in the collections of the San Diego Natural History Society (SDSNH) collected by C. B. Perkins.

The larger new anole may be named, with reference to its heavily spotted throat:

Anolis maculigula, new species
(Figs. 1–3)

Holotype: LACM 42150, adult male.

Type locality: Quebrada San Lorenzo, tributary of the Río Arquía near the small town of Belén (6° 15′N 76° 39′W), about 10 to 15 km upstream from the junction of the Río Arquía with the Río Atrato, western Antioquia, Colombia, N. J. Scott coll., 17 April 1968.

Paratypes: Antioquia: LACM 42142, 42144-49, 42151-54, same data as the type; ICN 5917, Camp Pegadorcito (Ingeominas), (about 6° 42′N 76° 27′W,) on the height of the Cordillera Occidental between Frontino on the south and Dabeiba on the north, Río

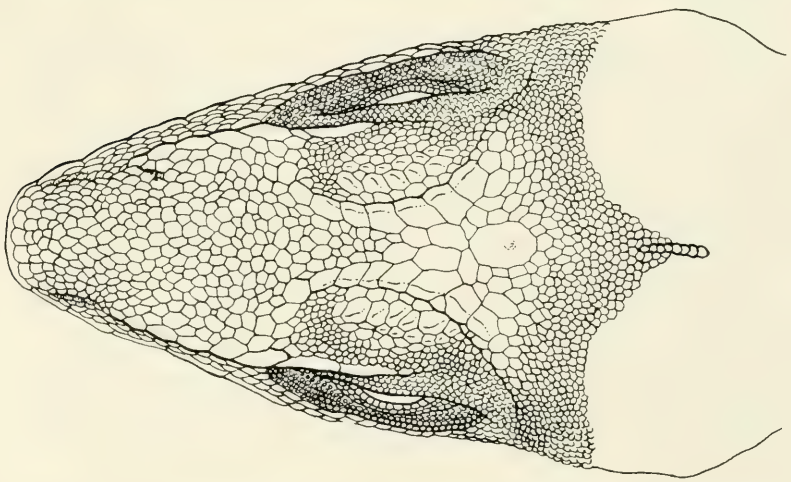


Figure 1. *Anolis maculigula,* new species. Type, LACM 42150. Dorsal aspect of head.

Figure 2. *A. maculigula*, new species. Type, LACM 42150. Lateral view of whole animal.

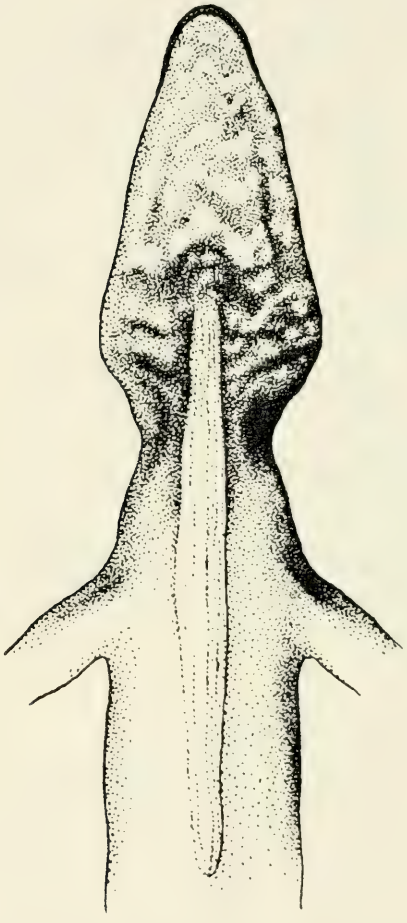


Figure 3. *A. maculigula,* new species. Type, LACM 42150. Throat pattern.

Amparradó, 805 m elevation, Juan M. Renjifo and Vladimir Corredor coll., 16 September 1981; ICN 5918, at the first stream beyond Pegadorcito, J. M. Renjifo and V. Corredor coll., 14 September 1981; CSJ 308-309, Urrao, Parque Las Orquídeas, Horatio Echeverri coll., 21 May 1981; CSJ 431, 445, 447, Urrao (Río Calles), Marco A. Serna and Horatio Echeverri coll., 10-12 July 1983.

Diagnosis. An alpha anole of moderate size related to *A. eulaemus* Boulenger and, like the latter, having small head scales and narrow digital dilations, but differing in having fewer scales between the supraorbital semicircles and between the semicircles and the interparietal, differing also in color, habits and habitat.

Description. Head. Head scales small, pustulose, swollen, keeled. Twelve to 19 scales between the second canthals. Eight to 11 scales bordering rostral posteriorly. Anterior nasal separated from rostral by one or two scales.

Two to three scales between supraorbital semicircles. A few supraocular scales distinctly enlarged, no well-defined supraocular disk. One to two elongate supraciliaries on each side followed by granules. Canthus distinct, seven canthal scales, the second longest. Eight to 11 loreal rows, scales small, subequal.

Temporal and supratemporal scales granular. A very indistinct double row of enlarged granules at margin between temporal and supratemporal areas. Scales around interparietal enlarged, interparietal larger than or about equal to ear, separated from supraorbital semicircles by one to three scales on each side or in contact.

Suboculars separated from supralabials by one row of scales, posteriorly grading into temporal granules, anteriorly diminishing gradually in size in front of eye. Seven to ten supralabials to center of eye.

Mentals wider than deep, in straight line contact with eight to ten scales between infralabials, grading in size from the infralabials toward the center. Sublabials not clearly differentiated. Central gular scales small, swollen, even conical, grading laterally into much larger scales.

Trunk. Two to three middorsal rows slightly enlarged, tricarinate, imbricate, grading into small, keeled but juxtaposed flank scales, showing small granules between them. Ventral scales equal to or smaller than the middorsals, smooth, flat or swollen, subimbricate or juxtaposed, sometimes showing small granules.

Dewlap. Large in male, extending onto first third of belly. Edge scales ca. equal to ventrals. Lateral scales in rows, several scales across, widely separated by naked skin. Barely indicated in female.

Limbs and Digits. Largest arm and leg scales larger than ventrals and uni- to multicarinate. Supradigital scales multicarinate. Sixteen to 22 lamellae under phalanges ii and iii of fourth toe.

Tail. Distinctly compressed to very strongly compressed, most strongly in the adult male, a low crest of unicarinate scales, the crest scales at least 2X those of the lateral rows. The other caudal scales uni- to multicarinate. No enlarged postanals in male.

Size. The male type measures 98 mm snout to vent. A topotypic male measures 72 mm, while the largest topotypic female is 73 mm snout-vent length. The male from Urrao (CSJ 308) is 107 mm snout to vent; the unregenerated tail is 215 mm long. The female (CSJ 309) from the same locality has 75 mm snout-vent length.

Color in Life. Normal Scott has provided notes from life for topotypic specimens. "Adult male: Dorsum with an obscure pattern of five dark brown blocks separated by lighter gray brown areas and broken by, on each side, a dorsolateral stripe of the same color. Dorsal crest paler and green. Tail and legs banded with dark gray brown and light gray green. On flanks a mixture of olive gray and orange flecks on a green ground. Side of head a mixture of orange and gray flecks, lips mottled and with blue flecks. Soles of feet olive brown. Throat with a series of orange and blue stripes. Chin mottled with orange, blue and gray, the blue predominant. Iris as in female but white ring tinged with green. Dewlap color complex: base with orange stripes on a blue gray ground, anterior third pale bluish rose, posterior portion white becoming pale blue toward belly. Juveniles colored much as females but green brighter on head, neck and sides. Adult female: Dorsum dark gray brown with gray black bar, lighter areas on neck, head and legs greenish gray. Sides mottled gray, olive green and black with a few light gray punctations. Side of head mostly greenish. Venter clear white, throat mottled green and white, underside of head patterned with white and gray, the chin with green and gray. Iris dark brown enclosing a narrow white ring."

Juan Renjifo in a note to Stephen Ayala reports the color in life of the Amparradó *maculigula* (translated): "Color green (lichenate) with dark blotches on the back, the first above the shoulders. A blotch at the shoulder dark with a white spot in the center."

Color in Preservative. Color now differs substantially from that reported for the fresh specimens. All blues, pinks and greens are gone. There are only light and dark grays but the complex pattern is retained. The dark crossbars of the middorsum contain light spots and the lower flanks tend to be vermiculate. The throat is boldly to weakly vermiculate, less strongly vermiculate in males than in

females, in which the heavily marked throat contrasts strikingly with the light and unmarked belly. The skin of the throat fan is gray.

Habitat and Habits. The type locality, Quebrada San Lorenzo, is described as a stream about 10 m wide with occasional waterfalls, with a moderately steep gradient and huge boulders. *A. maculigula* was most common where there were 3 to 4 m diameter moss-covered boulders at the head of pools, when first seen most were on the upstream vertical face of the boulders in the spray zone and tried to escape under the overhanging edge of the boulders. In Quebrada San Lorenzo the smaller (*lionotus* group) species also occurred but was less common. (See further below.) No comparable details are available for the habitat of ICN 5917 and 5918, but the latter specimen is reported as on rocks in a stream.

Comparisons. *A. maculigula* is clearly an alpha anole; a caudal vertebra dissected from a broken tail shows no trace of transverse processes. It is referred to the *aequatorialis* species group on the basis of very small head scales, large size and narrow digital dilations. Since its toe pads are "raised," i.e., overlap distally the proximal scales under the first phalanx, it is further referred to the *eulaemus* subgroup in contrast to species with pads "not raised," i.e., not overlapping but continuous with the scales of the first phalanx. (The latter are the *aequatorialis* subgroup.)

Within the *eulaemus* subgroup, in which there are a confusing number of undescribed populations, *A. maculigula* is distinctive in its pustulose head scales, its small ventrals, usually smaller than the small dorsals, and in the relatively large size of the interparietal which is almost always larger than the ear, in the very compressed tail and in a distinctive coloration. It may well be unique among the known eulaemoid forms in its semiaquatic habits also. Certainly no other member of the group shows so compressed a tail or *maculigula*'s tendency to a lined pattern.

The second and smaller species may very appropriately receive the Latin name that means "user of the same stream":

Anolis rivalis
(Figs. 4–7, 12, 14)

Holotype: LACM 42124, adult male.

Type locality: Belén, Río Arquía, Antioquia, Colombia (6° 15'N, 76° 39'W), Norman J. Scott coll., 17 April 1968.

*Paratypes: Antió*quia: LACM 42128-133, 42135, 42137-139. MCZ 115720-722 from the type locality, Norman J. Scott coll.; LACM 42125-127, 42141, 45002-07, 51540, Finca Los Llanos, Río Arquía, Philip Silverstone coll., 1968; ICN 5912, Camp Pegadorcito (Ingeominas), 45 minutes by helicopter from Medellín, on the height of the Cordillera Occidental between the towns of Frontino to the south and Dabeiba to the north, Río Amparradó, 805 m elevation, (about 6° 42′N, 76° 27′W,) Juan M. Renjifo and Vladimir Corredor coll., 13 September 1981; ICN 5913, Filo Amparradó, the same area and collectors, 16 September 1981; ICN 5914, Camp Chontaduro, same area and collectors, 9–12 September 1981; ICN 5915, same area and collectors, 14 September 1981. *Chocó*: LACM 72766, 72772, MCZ 100353, Alto de Buey, P. Silverstone coll., 1968; ICN 4053, Quebrada Mutatá, 200 m, northern base of Alto de Buey, C. W. Myers, John Daly and Michael G. A. Hill coll., 18–24 October 1978; SDSNH 31163, "Port Utria," = Puerto Utria (6° 02′N, 76° 23′W), C. B. Perkins coll., 25 February 1938.

Diagnosis. A member of the *lionotus* group of beta anoles, differing from the remainder of the group in the combination of small but not minute head scales (13 to 18 across snout between second canthals), one to two rows of scales between the supraorbital semicircles, interparietal in contact with the semicircles or separated by no more than two rows of scales, and by a zone of moderately large, indistinctly keeled, flat scales on the middorsum in 11 to 18 rows.

Description. Head. Scales small, uni- to multicarinate. Thirteen to 18 scales across snout between second canthals. Seven to nine scales border rostral posteriorly. Anterior nasal scale separated from rostral by one scale. Nine scales between supranasals. Scales in posterior portion of frontal depression smaller than those anteriorly placed.

Supraorbital semicircles separated medially by one to three scales, in contact laterally with the largest scales of the supraocular disks which consist of a variable number of wrinkled or keeled scales, a few of which may be much larger than the others. One to three elongate supraciliaries continued posteriorly by a series of smaller scales. Canthus distinct, canthals 9. second largest. Six to 10 loreal rows, lowermost largest.

Temporals small and flat, not granular. A distinct double supratemporal row, dorsad of which nearly granular scales grade

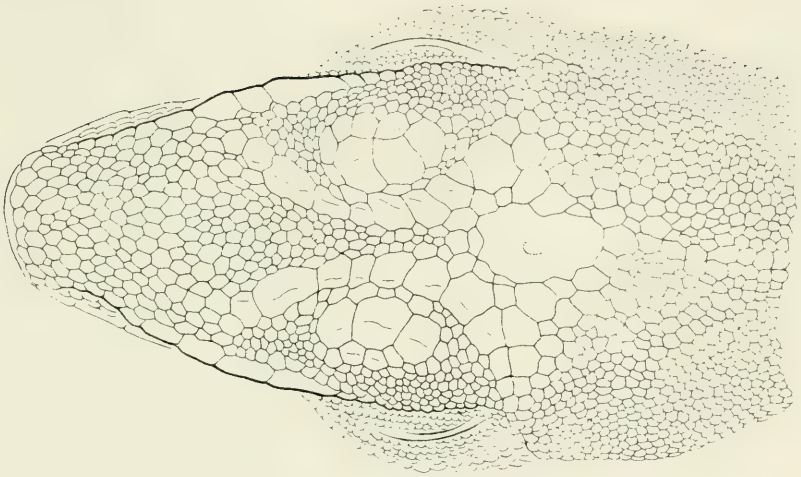


Figure 4. *A. rivalis,* new species. Type, LACM 42124. Dorsal aspect of head.

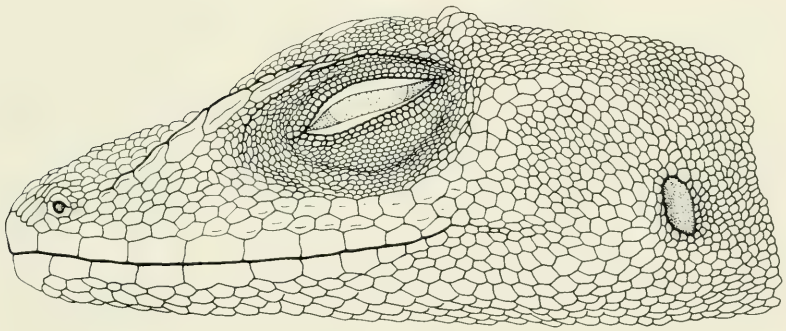


Figure 5. *A. rivalis,* new species. Type, LACM 42124. Lateral aspect of head.

into the flat scales surrounding the large interparietal, usually larger than ear and in contact with the semicircles or separated by one to two scales. Scales posterior to interparietal not different in size from middorsals but grading into smaller nape scales which then grade posteriorly into the dorsals. Suboculars weakly keeled, narrowly in contact with supralabials or separated by one scale row, grading

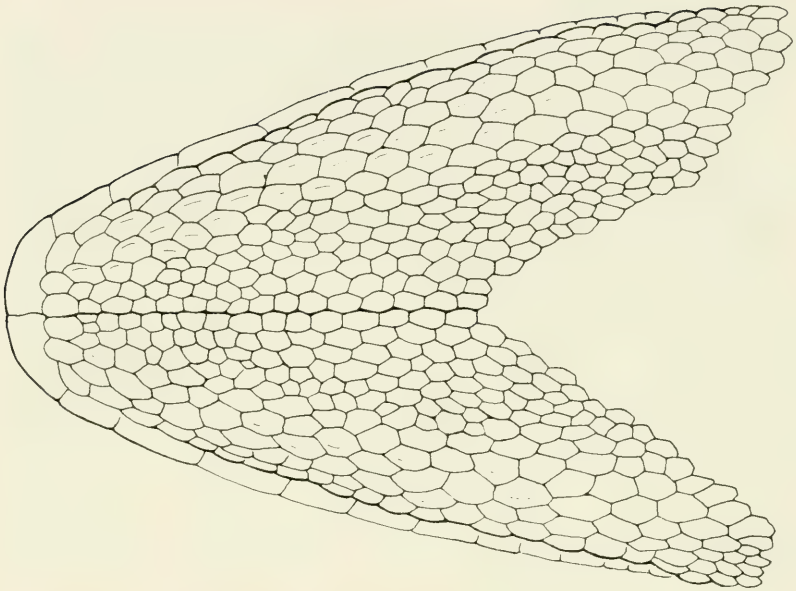


Figure 6. *A. rivalis,* new species. Type, LACM 42124. Ventral view of chin.

anteriorly into loreals, posteriorly more sharply distinct from the temporals. Six to nine supralabials to the center of the eye.

Mental divided, wider than long, in contact with six or seven scales between infralabials. Gular scales smallest medially, quadrate, swollen.

Trunk. Middorsal scales flat, hexagonal, wrinkled, in ca. 11 to 17 rows, grading quite gradually into subgranular flank scales, larger in the center of the body than on the nape, becoming slightly smaller again in the sacral region and on the base of the tail. Ventrals smaller than dorsals, keeled, imbricate.

Dewlap. Moderate, extending onto first third of belly, lateral scales weak, in densely packed rows, edge scales keeled, slightly larger than ventrals.

Limbs and Digits. Scales on limbs strongly unicarinate except at knees and elbows where they are multicarinate. Supradigital scales multicarinate. Twelve to 18 scales under phalanges ii and iii of fourth toe.

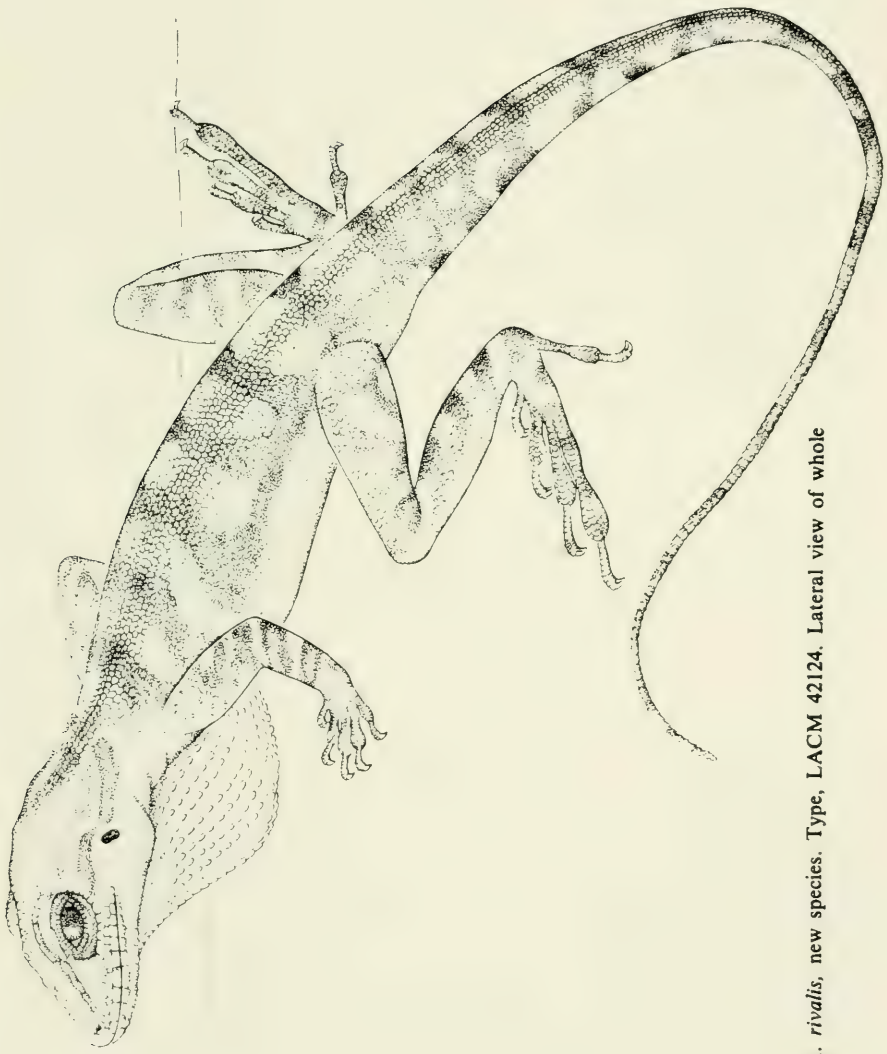


Figure 7. *A. rivalis*, new species. Type, LACM 42124. Lateral view of whole animal.

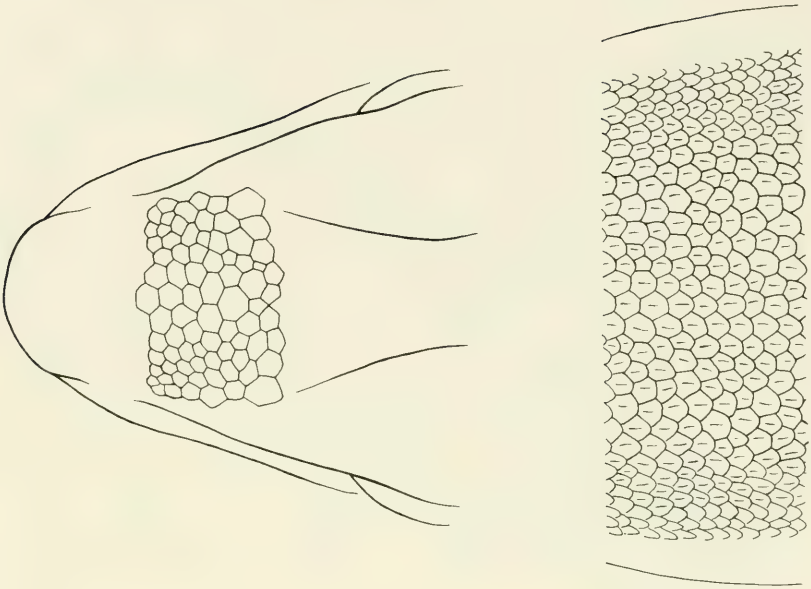


Figure 8. *A. oxylophus,* KU 34262. Frontal and middorsal scales.

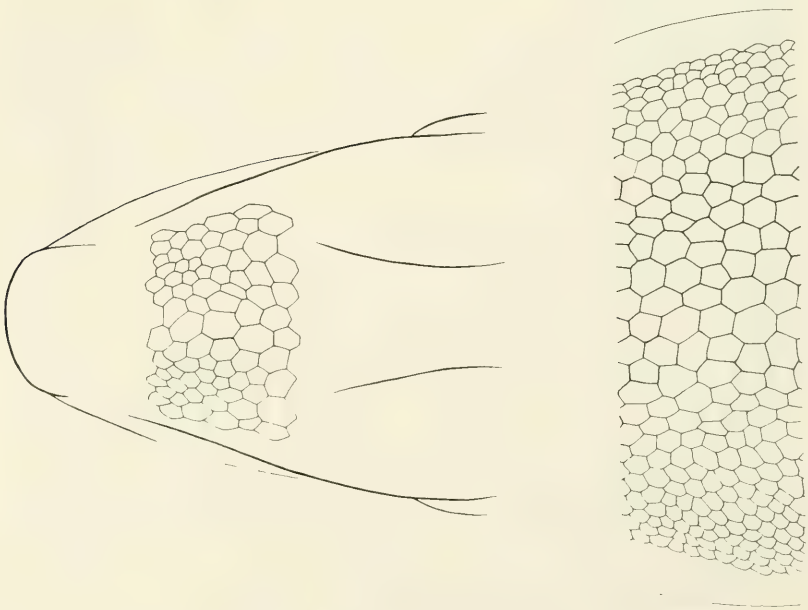


Figure 9. *A. lionotus,* KU 75951. Frontal and middorsal scales.

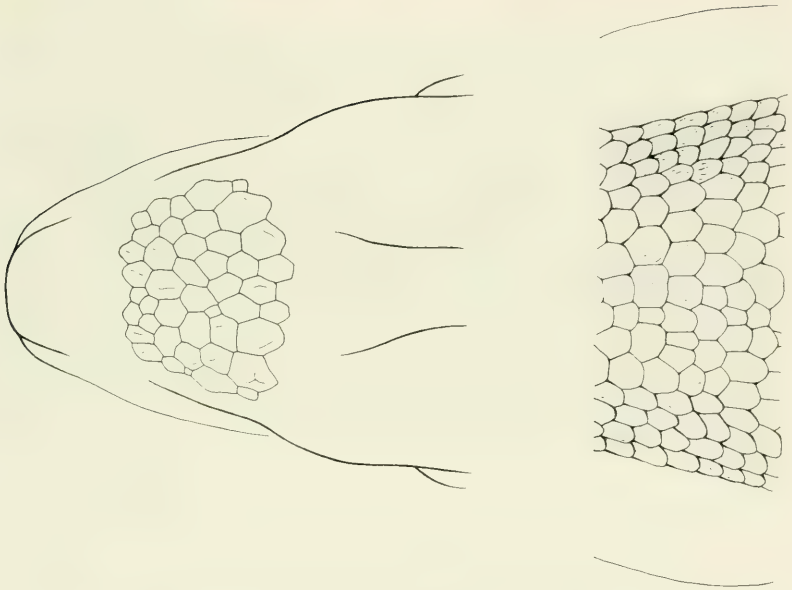


Figure 10. *A. macrolepis,* MCZ 133000. Frontal and middorsal scales.

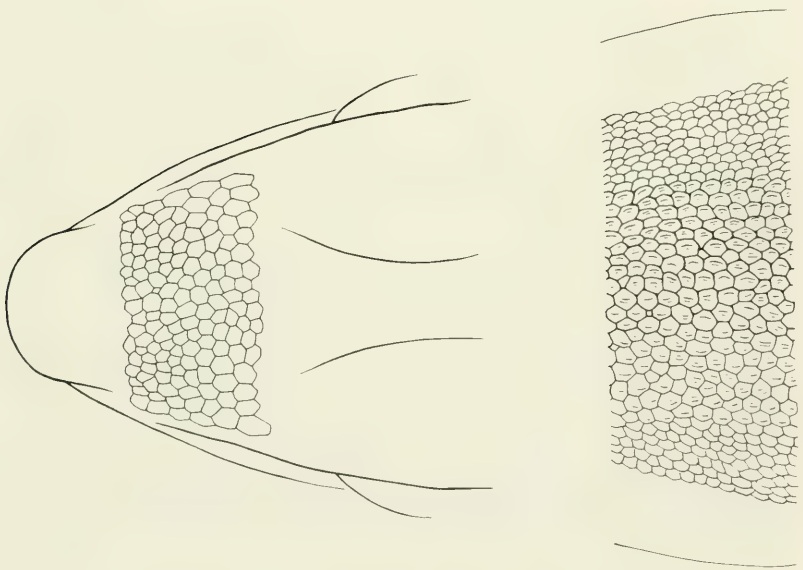


Figure 11. *A. poecilopus,* KU 113249. Frontal and middorsal scales.

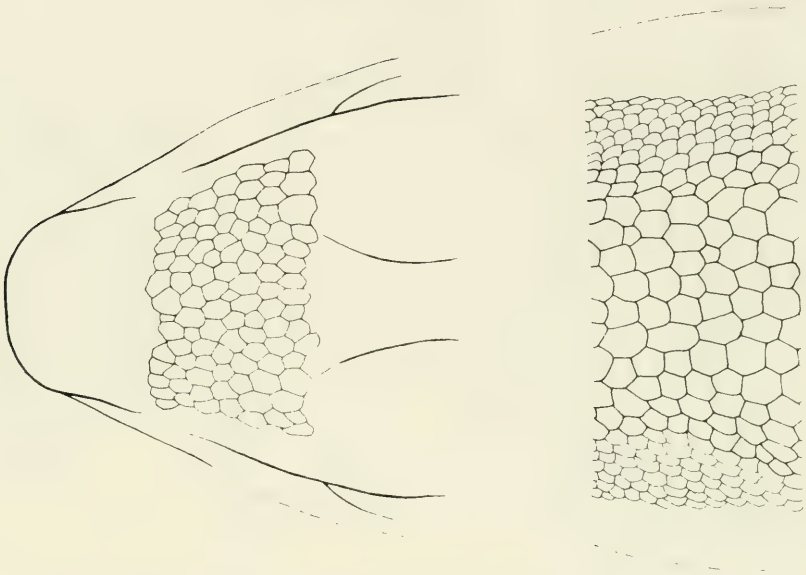


Figure 12. *A. rivalis,* LACM 42129. Frontal and middorsal scales.

Tail. Compressed without dorsal crest. Verticils indistinct. Enlarged postanals absent.

Color as Preserved. Brown with darker flanks. Middorsum banded. Two narrow light lines on sides, one above shoulder, one starting at axilla. Spotting on lower flanks. Limbs banded. Belly and throat white or very weakly spotted. Dewlap white. Nape white to above level of ear where a darker margin sets it off against the dorsal light brown.

Size. The type male is 62 mm in snout-vent length. MCZ 115722 and LACM 42138, topotypic males, are each 64 mm snout to vent.

Color in Life. Scott provides color notes on the topotypic specimens: "Adult male: Dorsum dark brown with thin green brown vertical bands on flanks. Several stripes from axilla to groin, the lower ones heavily suffused with red. Light areas on sides dusty rose. Venter yellowish white with heavy red suffusion on sides of abdomen, throat and underside of head. Iris dark chestnut enclosing a narrow yellow ring. Dewlap solid orange. Adult female: Dorsum

Figure 13. *A. rivalis* from Quebrada Mutatá, 200 m, northern base of Alto del Buey, Chocó, Colombia. Photo by C. W. Myers.

as in male but with only a faint hint of red suffusion. Light areas of head white becoming green on snout. Venter yellowish white. Dewlap area with pale orange spot, throat anteriorly white. Iris as in male."

Notes by C. W. Myers on the specimen obtained from Quebrada Mutatá record the following colors: "Brown, changeable to brownish green, with lateral line and lower side of neck dirty white. Throat gray, dewlap light orange, venter greenish gray. Iris brown. Tongue light gray."

Juan Manuel Renjifo has supplied color notes on ICN 5912 from the Río Amparradó region: Greenish brown with bars of lighter greenish brown forming chevrons on the middle of the back. Labials and flanks rosy salmon. Venter yellowish cream. Gular sac white.

One entry in Scott's field notes cites an unspecified *rivalis* from Belén as having an orange dewlap. There would appear to be a range of dewlap colors in this species.

Habitat and Habits. At Quebrada San Lorenzo, Scott reports *A. rivalis* both to be less common and to occur on small rocks near the bottom of pools rather than on the huge moss covered boulders preferred by *A. maculigula.* They escaped by running from rock to rock over the water surface. Some were taken at night sleeping on

vegetation overhanging the stream. He specifically mentions (letter of February 28, 1979): "Quebrada San Lorenzo was the only place where I got both aquatic species. Nearby Quebrada Barrero had less water and seemed to have only the "lionotus" [= *rivalis*] type."

The single specimen of *A. rivalis* obtained by the Myers group in 1978 was again found in a quebrada, but the notes do not cite any larger aquatic species.

Renjifo in his field notes does not mention close or co-occurrence of the two species and confirms the semi-aquatic habits of *rivalis* in the Amparradó region. He cites ICN 5912 as (translated) "in forest on trunk above the stream, ½ meter above ground level;" ICN 5914 "in stream on a stone;" ICN 5915 "sleeping on rocks in the stream alongside the current;" and ICN 5918 "in stream....on rocks."

Comparisons. *A. rivalis* is a member of the beta series and of the *lionotus* species group.

The latter is a series of taxa (the other referred species: *oxylophus* Cope, 1875, *lionotus* Cope, 1861, *poecilopus* Cope, 1862, *macrolepis* Boulenger 1911) that extend from Nicaragua to Ecuador, replacing one another with minimal or no overlap, so far as known. A sixth taxon belonging to this group occurs in northwestern Ecuador and southwestern Colombia. It will be described by Kenneth Miyata. All are characterized ecologically by "aquatic" habit and riparian habitat and (usually) by a zone of enlarged dorsal scales, more or less similar in size over an area of 14 to 20 rows, then grading laterally into the flank scales. They have also small keeled ventrals and a more or less well developed flank stripe.

The species of this group ring the changes on just a few morphological characters: the size of the head scales, the number of scale rows between the supraorbital semicircles, the number of scales between the interparietal and the semicircles, the size of supratemporal and nape scales, and the size and also the keeling or lack of keeling of the middorsals. Each of these characters varies independently, and adjacent species tend to be sharply distinct in one or more features.

No revision of the *lionotus* species group exists nor has South American *macrolepis* been recognized as a member of it until recently (Williams, 1976).

Boulenger (1911) in describing *macrolepis* did, indeed, associate it with *poecilopus* but also suggested a relationship to *notopholis* (*humilis* species group), to which it is only superficially similar.

Figure 14. Map: Localities for semiaquatic anoles in Colombia and adjacent Panama.

Table 1. **Scale characters within the *Anolis lionotus* species group.**

	oxylophus (Costa Rica, Nicaragua)	*lionotus* (Panama)	*poecilopus* (Panama, Colombia)	*macrolepis* (Colombia)	*rivalis* (Colombia)
head scales	moderate	moderate	minute	moderate	small
number of scales between second canthals	8–14	8–12	14–21	7–10	13–18
supraocular scales	moderate to *large*, keeled	moderate to *large*, keeled	moderate, keeled	large, wrinkled	moderate, wrinkled
scales between semicircles	1–3	1–3	2–5	0–2	0–3
interparietal/ear	ca. =	ca. =	ca. =	>	ca. = or >
circum-interparietal scales	*large*	*moderate to large*	anteriorly moderate to small, posteriorly *minute*	large	moderate to large

number betwen ip and semicircles	1–3	1–2	2–5	0–2	0–2
supratemporal scales	large	moderate	minute	moderate to large	small to moderate
nape scales/dorsals	=	(<)	< smaller than small dorsals	=	distinctly <
dorsal zone of enlarged scales	moderate, flat, weakly keeled, or smooth, weakly imbricate	large, flat, smooth, juxtaposed	small with raised edges and central keel	large, keeled or wrinkled, weakly imbricate	large, keeled or wrinkled, weakly imbricate
number of enlarged dorsal rows	19–22	11–16	13–24	11–17	8–15
dorsal scales/ventrals	ca. =	ca. 2x >	ca. =	>	>
lamellae 4th toe	13–17	14–16	12–19	13–16	12–18
adult male size	72	73	68	62	64

Taylor (1956) in his discussion of the lizards of Costa Rica called attention to the discrepancies between the type description of *lionotus* Cope, 1861 (with a type locality in Panama) and that of *oxylophus* Cope, 1875 (without exact locality but presumably from Costa Rica), which was supposedly a synonym. However, lacking Panamanian specimens, he followed then and current usage in applying the name *lionotus* to Costa Rican animals. My own examination of most of the material available in American museums shows significant differences between eastern Panamanian and western Panamanian and Costa Rican-Nicaraguan specimens. Campbell (1973) noted the character of true *lionotus* that has most impressed me: dorsal scales about twice the size of the ventrals. In *oxylophus* (as in *poecilopus*) the dorsals and ventrals are about equal but in *poecilopus* the dorsals are strongly keeled, in *oxylophus* smooth or weakly keeled. Table 1 reports the characters distinguishing members of this group.

The new species is distinguished from all other members of the *lionotus* group by a combination of characters: small but not minute head scales, few scales between the supraorbital semicircles, small to moderate supratemporal scales, nape scales distinctly smaller than the enlarged dorsals which are large, larger than the ventrals, wrinkled or weakly keeled and weakly imbricate. From *poecilopus* it is distinguished by its much larger middorsals, fewer rows between the supraorbital semicircles and its larger circum-interparietal scales. From *macrolepis* it is distinguished by its somewhat larger middorsals, the nape scales distinctly smaller than the large middorsals (rather than subequal) and by smaller head scales.

Discussion. The sympatric occurrence of two semiaquatic anoles is not unique: within the *lionotus* group there is the example of the local sympatry of *poecilopus* and *lionotus* in the vicinity of the Panama Canal (Campbell, 1973). In this case the overlap zone is suspected to be narrow, but knowledge of the distributions is not adequate to demonstrate this. In the case of *poecilopus* and *lionotus,* the two overlapping species are very different within the group in dorsal and head scale size. (In general, in the *lionotus* group, although the species are primarily allopatric, the differences summarized in Table 1 are greater in adjacent than in distant taxa.)

The two sympatric semiaquatic species here described are quite different in their affinities, belonging to different sections of the genus *Anolis.* They are adequately different in scale characters but

not quite so strikingly as the most different species pairs *within* the *lionotus* group. The similarities in habits, in the pronounced flank stripes, and in the strongly compressed tails, are indeed more impressive than their differences.

But these similarities are parallels only and are seen in other semiaquatic anoles not at all closely related, as Schwartz has demonstrated in describing a taxonomically quite isolated semiaquatic anole from Hispaniola (Schwartz, 1978). The semiaquatic anoles, except for the allo-parapatric series that constitutes the *lionotus* group, are not at all a lineage, but only an ecomorph in the sense of Williams (1972, 1983).

ACKNOWLEDGMENTS

I am indebted to the curators who have provided me the opportunity to describe the new species: John Wright and Robert Bezy of the Los Angeles County Museum, Pedro Ruiz of the Instituto de Ciencias Naturales, Bogotá, Colombia and Gregory Pregill of the San Diego Natural History Society. Norman Scott and Charles Myers have allowed me to quote from their field notes, and Pedro Ruiz has transmitted the field localities and observations of Juan Renjifo and Vladimir Corredor. Stephen Ayala has commented on the manuscript and provided the map which compares the distributions of Colombian aquatic anoles. Laszlo Meszoly has done the illustrations. The photograph of *A. rivalis* was provided by Charles Myers.

LITERATURE CITED

Boulenger, G. A. 1911. Description of new reptiles from the Andes of South America, preserved in the British Museum. Ann. Mag. Nat. Hist. ser. 8, **8**: 19–25.

Campbell, H. W. 1973. Ecological observations on *Anolis lionotus* and *A. poecilopus* (Reptilia, Sauria) in Panama. Amer. Mus. Novitates, No. 2516, pp. 1–29.

Cope, E. D. 1861. Notes and descriptions of anoles. Proc. Acad. Nat. Sci. Phila., **1861:** 209–215.

_____. 1862. Contributions to Neotropical saurology. Proc. Acad. Nat. Sci. Phila., **1862:** 159–188.

_____. 1875. On the Batrachia and Reptilia of Costa Rica. J. Acad. Nat. Sci., **8:** 93–157.

Schwartz, A. 1978. A new species of aquatic anole (Sauria, Iguanidae) from Hispaniola. Ann. Carnegie Mus., **47:** 261–279.

TAYLOR, E. 1956. A review of the lizards of Costa Rica. Univ. Kansas Sci. Bull., **38:** 3–222.

WILLIAMS, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. Evolutionary Biology, **6:** 47–89.

———. 1976. South American anoles: the species groups. Pap. Avuls. Zool. S. Paulo, **29:** 259–268.

———. 1983. Ecomorphs, faunas, island size and diverse end points in island radiations of *Anolis* pp. 326–370, 481–484. *In* Huey, R., E. Pianka, and T. Schoener (eds.), Lizard Ecology - Studies of a Model Organism, Harvard University Press, Cambridge, Mass.

MUS. COMP. ZOOL
LIBRARY
MAR 18 1985
HARVARD
UNIVERSITY

B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 7 SEPTEMBER 1984 NUMBER 479

AGONISTIC AND COURTSHIP DISPLAYS OF MALE *ANOLIS SAGREI*

MICHELLE P. SCOTT[1]

ABSTRACT. Male *Anolis sagrei* perform a dewlap fanning display and four different bobbing displays in agonistic and courtship encounters. Only one of the bobbing displays has a species-specific, stereotyped pattern. The total number of bobs and the number of bobs in each unit of this display and the use of the dewlap showed considerable variability both within and between individuals. The frequency distribution of the type of display used in aggressive encounters showed more inter- than intra-individual variability. Dewlap fanning displays were used at a relatively higher frequency before crests were raised, but the dewlap was used with the bobbing display at a relatively higher frequency by males after the erection of crests. Submissive animals displayed less frequently overall and were more apt to use a dewlap fanning display, but they were less apt to use the dewlap with a bobbing display than a dominant male. Male *A. sagrei* were less apt to use the species-specific stereotyped pattern in courtship than in agressive encounters. The "jiggle" bob display immediately preceeded half of the attempted matings. A dewlap fanning with erect posture was associated with the termination of a copulation.

INTRODUCTION

The brightly colored dewlaps and stereotyped bobbing displays of males of the iguanid lizard genus *Anolis* may communicate information regarding species, sex, reproductive state, dominance and territorial status, intentions, and level of arousal. Dewlap color alone sometimes does not appear to be an important element in species recognition and female choice for the solitary anole *A. carolinensis* (Greenberg and Noble, 1944; Crews, 1975a). However, in a complex *Anolis* fauna, color and dewlap proportions may

[1]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

provide redundant information for species recognition (Williams and Rand, 1977). Jenssen's work (1970a) with *Anolis nebulosus* indicates that the male's species-specific bobbing display does indeed play a significant role in sexual selection and female choice.

In examining anoline displays, recent researchers have focused on the degree of stereotypy (the amount and possible significance of variability within and among individuals) and the complexity of display repertoires of different species. Displays may vary either in temporal patterns or by the presence or absence of various components within the display. Species differ considerably in the amount of stereotypy of their displays, and the source of variability may be intra-individual or between individuals (Jenssen 1978). *Anolis carolinensis* (Crews, 1975b), *A. aeneus* (Stamps and Barlow, 1973), and *A. nebulosus* (Jenssen, 1971) have very stereotyped displays. Each individual performs a consistent display, but there is variability between individuals. Different populations of *A. nebulosus* have been examined and still further variability between populations was found. Other species, however, like *A. limifrons* (Jenssen and Hover, 1976) show greater intra-individual variability than inter-individual differences. At the extreme, almost all (97%) of the variability of *A. townsendi* displays is attributable to intra-individual variation (Jenssen and Rothblum, 1977). *Anolis opalinus,* on the other hand, was found to be almost completely lacking stereotypy at any level, individual or population, in that there was no single discrete display pattern. However, 75% of the analyzed displays fit a theme which explained the highly variable bob number and display cadence (Jenssen, 1979).

The complexity of the display repertoire of a species is another important feature. Researchers (e.g., Carpenter and Grubitz, 1961) first described only two basic types of displays, a courtship pattern of rapid head bobs and a species-unique "signature" pattern. The latter type was originally labeled an "assertion" display that, with modifiers, blends into a "challenge" display (Carpenter, 1967; Jenssen, 1970b, 1977; Crews, 1975b). Typically, if other display types were described, they consisted of the signature display plus modifiers (e.g., four-legged push-up posture preceding dewlap fanning), or they may be characterized by a different coordination of the dewlap extensions during the head bob sequence. Recently, researchers have found greater complexity in the display repertoire of some anoles (Hover and Jenssen, 1976; Jenssen and Rothblum,

1977). *Anolis aeneus, A. limifrons,* and *A. townsendi,* for example, have several clearly distinct display types which differ not just by the modifiers or the context in which they appear, but also by different bob patterns.

This paper described the display repertoire of male *Anolis sagrei* in agonistic and in courtship situations. A description and analysis of the species-specific stereotyped display and its variable elements are given. An attempt is made to analyze these displays and their modifiers in terms of the social context in which they appear and the effect they have on conspecifics. The possible role of the species-specific signals used in sexual selection is discussed.

MATERIALS AND METHODS

Anolis sagrei has a wide distribution, occurring on Cuba, Jamaica, the Bahamas, Little Cayman, Cayman Brac, Swan Island, and coastal areas of Mexico and Belize, and has recently been introduced into Florida (Williams, 1976). It occupies a relatively open habitat. During the breeding season, males and females are strongly territorial. A male territory has been described by Evans (1936) as at least 50 m^2 and containing up to three females. In cultivated areas, it is typical for males to occupy a hedge row or fence at approximately 6 m intervals (Evans, 1936; Scott, personal observation).

Twenty males (55–62 mm snout to vent length), 12 females and 8 juveniles were collected near the Universtiy of South Florida, Tampa, in May 1979 when the mature males and females were sexually active.

The lizards were held in experimental cages of two designs. In Design 1, one large male, a juvenile male and two to three females inhabited an aquarium 75 cm long × 32 cm deep × 45 cm high. Two of these aquaria so arranged were placed end to end with a removable opaque divider between them. Each contained a live plant and a prominent perching branch. The far side of each aquarium was covered by bark which was also favored as a perching site. Thus, when the opaque divider was removed, the two territorial males could see each other but were physically separated by a double pane of glass. In this design, 5 pairs of 10 different males were tested against each other three to five times. In Design 2, a wire cage 47 cm long × 51 cm deep × 39 cm high was divided in half

longitudinally by a removable opaque partition. A single large male was housed in each half, which also contained a plant, a perch, and a bark wall. In these cages, the animals were in physical as well as visual contact with each other when the partition was removed. In this design, three pairs of six different males were effectively tested against each other only once since subsequent tests would have been declared "no contest" at the outset by the participants. These wire cages were kept in Sherer-Gillet environmental chambers with transparent doors. All animals experienced a constant environmental regime of 14L:10D photoperiod and a corresponding temperature cycle of 32:23°C. All animals received food (mealworms and crickets) and water *ad lib.* Observation of the aquaria animals in Design 1 was made from behind a cardboard blind to ensure that the displays were directed at conspecifics and not the observer. The animals in the lighted environmental chambers of Design 2 were observed in a darkened room, making the observer relatively inconspicuous. The cages were arranged in each case so that no animal could see a conspecific except those in its experimental setup. When the partition was in place males were only occasionally observed displaying at the juveniles or females. Males were housed individually before they were placed in the experimental cages.

All males were allowed at least one week to acclimate to a new cage before testing was begun. Agonistic tests were at least 15 minutes long and continued 5 minutes after the situation appeared stable (that is, when there was no change in positions and display types used by the two animals). Courtship tests were terminated when the animals finished copulating.

Male agonistic behavior was studied in both types of cage designs with the opaque dividers removed. Males in the aquaria of Design 1 were repeatedly tested against each other whereas those in the wire cages of Design 2, which allowed physical contact, only met once because, once beaten, the subordinate animal did not display but retreated. Courtship behavior was observed only in the cages of Design 2; the partitions were left intact and a female was introduced into a wire cage which housed a single male.

Parameters of male behavior were recorded with a 10 channel Esterline Angus operation recorder Model A. Displays were taped with a Sony video camera AVC 3210 with a 75 mm f12.5 lens and analyzed with a Sony videorecorder AV 3650 with which the tapes

could be slowed to 8% actual speed. The head and dewlap movements were transcribed onto a strip of acetate by running the acetate in front of the video screen at a constant known speed, using the gears of the event recorder and following the action with a felt tipped pen placed on the rostrum of the videotaped lizard. The time framework could be superimposed on the tracing making corrections for the video recorder speed and the gear ratio of the event recorder. Only animals from the wire cages of Design 2 were videotaped because the T.V. equipment was less conspicuous to the subjects.

A total of 620 agonistic displays by 12 different males were observed in 18.8 hours. Two hundred twenty-nine displays of eight different courting males were observed in 12.4 hours. Thirty-one displays of three males in two entire agonistic events and three different males in entire courtship tests were taped and analyzed. Recording data on the video equipment and event recorder provided different benefits. When using the event recorder, the social context of the display and the response of the recipient could easily be included. In this way the meaning of the display could be defined by the response it provoked. With the video equipment it was possible to record data on the modifiers of the displays in fine enough detail to compare and discuss variability within and between individuals. The cadence of bobs could also be recorded to discriminate the type of bobbing display and to relate it to the social context.

For purposes of discriminating dominant and submissive behavior, the animals of all the tests in both cage designs were divided into two groups on the basis of their behavior at the end of the test. An animal was judged to have been acting dominant throughout the test if he was still facing his opponent at the end with an alert posture. Those anoles that ran from their opponent to the far side of the cage and had a posture low to the substrate were classed as submissive for the whole test. Since these classifications were somewhat subjective, borderline cases in which either animal showed a mixture of dominant and submissive behavior at the end of the test were not used in the following analysis. Within each group there was little variance in the frequency of each type of display performed (Table 1); therefore, for statistical purposes, data from all dominant males were pooled, as were those from all subordinate males.

Table 1. Frequency ± variance of displays by type per minute of animals judged at the end of the test to be dominant or subordinate.

	Dominant animals (N = 34)	Subordinant animals (N = 11)	Difference
Dewlap only	0.07 ± 0.01	0.07 ± 0.01	n.s.
Bob only	0.43 ± 0.06	0.21 ± 0.04	$t = 2.70$, $p < 0.01$
Bob + dewlap	0.16 ± 0.02	0.01 ± 0.00	$t = 3.49$, $p < 0.001$

Any encounter escalated (if it were going to) in a predictable fashion. Modifiers were added to displays and other behaviors appeared in the same order each time, as the states of arousal of the participants increased and their bodies became more tense. To facilitate analysis of behaviors and responses in agonistic encounters, confrontations were divided into three stages which were differentiated by changes of body posture. In the first stage, a male had not yet erected either a nucal or dorsal crest or laterally compressed his body and was said to be in state A. In the second stage, a male had both crests (state B) and in the third, most aroused stage, he had laterally compressed his body as well (state C).

Statistical tests used were t-test of proportions, arcsin transformed, to test the difference between the means of two samples and a one-way analysis of variance to examine the inter- and intra-individual variance in display stereotypy. Means are expressed ± the standard error.

RESULTS AND DISCUSSION

Displays and Modifiers

A display is a sequence of behaviors, usually performed in its entirety, which communicates information about the sender. In the following context, it refers to the change in amplitude over time of a lizard's head and/or dewlap and encompasses any consistantly associated stereotyped movements or postures. A modifier is a posture (static modifier) or movement (dynamic modifier) which is not always present with a particular stereotyped display but may be added (Jenssen, 1978). *Anolis sagrei* sometimes performed these modifying behaviors, particularly postures, separately from stereotyped head bob displays.

A brief description of the displays investigated follows. The frequency distributions of the display types, degree of stereotypy,

and information conveyed are all discussed later in the context in which the display was used.

Dewlap Fanning. The dewlap, which in Florida *A. sagrei* is bright orange with a yellow margin, is extended by the hyoid apparatus. The pattern and context of this action is extremely variable. It can occur as a single extension or in a fast or slow series of as many as 15 separate extensions. The series have no discernible pattern, and the display is used in all observed contexts and may be directed at a human observer as well as a male or female conspecific.

Bobbing. The head can be bobbed from the neck, from mid-body, or as a four-legged push-up. Bobs from the neck or mid-body can occur singly or in a series of a single posture, or the display may begin as bobs from the neck and finish as bobs from the mid-body. These postures may demonstrate increasing states of arousal in that order. Bobs with a four-legged push-up posture are not performed singly. These four-legged push-up bobbing displays are typically 8–10 bobs but may contain 18 to 20 and last as long as 30 seconds.

There are three different sorts of bobbing displays.

(A) *Anolis sagrei* can perform a species-specific stereotyped display which has a distinctive cadence to a series of bobs which may be called its "signature" display (Stamps and Barlow, 1973). It consists of four units: 2 quick initial bobs of increasing amplitude, a long bob, a short bob, followed by a series of 3 to 12 even-tempo bobs dampening in amplitude (Fig. 1). There may be variation in bob number of any unit of the pattern. If the dewlap is extended during the display, it always flashes on the third (long) bob and variably during the dampening series of bobs at the end. This signature display occurs in an assertion context (i.e., non-directed or low conflict situation), in both agonistic and courtship tests, and at every state of arousal.

However, sometimes this bobbing display does not consist of this characteristic pattern. It may, however, have some similar elements to the signature pattern such as a long bob accompanied by a dewlap extension followed by a short bob. These displays also may or may not be accompanied by dewlap extensions and without them as a marker, the elements similar to the signature pattern often could not be identified. For example, in the display illustrated by Figure 2, the dewlap extension at 5 seconds marks what might be the long bob followed by the short bob characteristic of the signature pattern but it is unrecognizable by the pattern of bobs alone. These displays also may occur in any context.

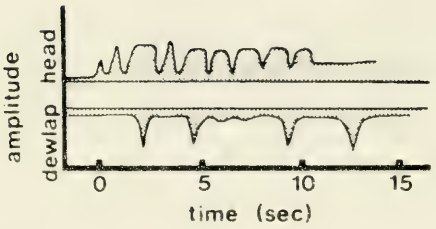


Figure 1. The signature display of *Anolis sagrei*.

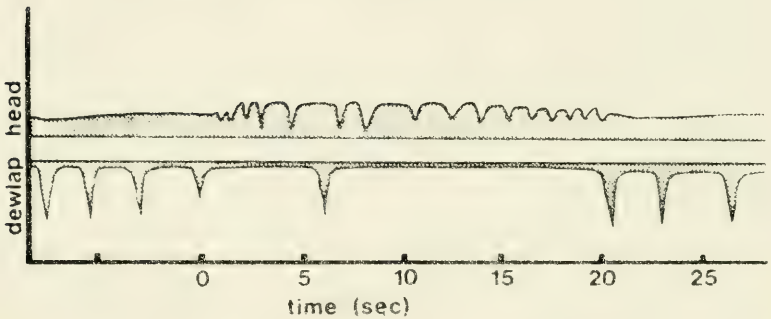


Figure 2. A typical example of a display that did not fit the signature pattern.

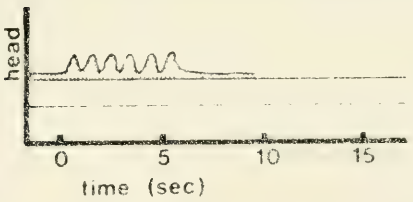


Figure 3. The quick rhythmic bobbing display.

(B) The second bobbing display is characterized by a quick (about 1–2/sec) rhythmic bobbing with no inter-bob pause and without any dewlap extension (Fig. 3). The amplitude of these bobs was less than that of the bobs of the signature display, and usually it was performed with the head and body close to the substrate. In these tests, 49 of 53 times it was performed by an animal in a submissive situation. However, it was occasionally (4 times)

performed by a highly aggressive dominant male in a context when the opponent had a submissive posture.

(C) The third type of bobbing display is jiggling action of the head. The amplitude of these bobs was very much less than that of other bobbing displays and the rate was much faster (8–10/sec). In these tests, all 34 times this display was used was in courtship situations and was performed by the male usually as he approached the female to take a neck grip prior to mating. It may be performed as a separate display or tacked on to the end of another.

Modifiers. Many different behaviors may be used to modify a display. Some were consistently used in a particular context and state of arousal and often caused a consistent response in the recipient and therefore these modifiers may impart specific information on the intent and motivation level of the animal displaying. See Table 2 for a list of modifiers frequently used, their social context, and state of arousal when used.

Male-Male Encounters

The encounters between two males were staged such that they would both be expected to act territorially. A total of 12 different males were used in 26 tests. In Design 1, the two aquaria which each housed resident males were sufficiently large that the males were often 150 cm apart when they first saw each other, so that in 45% of the 25 tests they escalated aggression (see below) and were only prevented from combat by the glass partitions. When these same two males confronted each other in future tests, both continued to act aggressively. The situation in the wire cages of Design 2 was different. The animals were less than 50 cm apart when they first saw each other, and there was no physical partition. In every instance the rank order of the two was quickly apparent when one male fled without a contest; there was no escalation of aggression. The physical proximity seemed to be a deterrent to bluffing by the less aggressive male and did not allow for a slow escalation of aggressive behavior and evaluation of each other.

The sequence of events in an escalating fight is typical of that described for other anoles (Crews, 1975b). Behaviors and modifiers to displays are added in a sequence that is predictable. In a aquaria of Design 1, males would display towards each other with first a nuchal crest and then a dorsal crest being erected. The whole body

Table 2. Modifiers used in displays of male *A. sagrei* and their context. The steps in escalation of an encounter from first display to conclusion (combat or neck grip) were consistently ordered (see text). The state of arousal refers to the stage of escalation.

Modifier	Display	Context	State of Arousal
Dewlap extension	Signature display	Assertion, courtship & aggression	All
Nuchal crest	Signature display or continued condition	Aggression	Moderate
Dorsal crest	Signature display or continued condition	Aggression	Mod. high
Lateral compression	Signature display or continued condition	Aggression	Highest
Engorged throat	Usually a continued condition but can accompany signature display instead of dewlap extension	Aggression	Moderate → highest
Tail lift	In 4-legged push-ups of signature display	Courtship & aggression	Mod. high → highest
Tail lash	Alone or with signature display	Aggression	Mod. high → highest
Tongue protrusion	Alone or with signature display	Aggression	Mod. high → highest
Lip smack	Alone or with signature display	Aggression	Moderate → highest
Slow approach	Jiggle display	Courtship	Highest

can then be laterally compressed. (Table 3 illustrates that these successive posture changes indicate increasing states of arousal.) As the lizard's body becomes more tense, the bobbing action becomes more exaggerated, from nods to two-legged push-ups to four-legged push-ups. At this point increasing intensity of arousal is signaled by behaviors other than the bobbing displays. The males approach each other either slowly or with a rush. They will orient head to tail, lunge, and threaten by gaping their mouths. Because the animals were either physically separated or unwilling to engage in combat, no staged fight in either Design 1 or 2 proceeded past this point, but in a natural setting the fight will end with jaw grappling and one being physically pushed off the branch and chased off (Scott, personal observation).

Table 3. The probability of an animal in an agonistic confrontation taking a more aggressive posture. A, B, and C are the states of arousal, and A → B is the probability of a male in the first state going to the second. An animal in state A has a body posture without nucal or dorsal crests or lateral compression of the body. An animal in state B has both crests and one in state C has crests and lateral compression.

	# tests	A → B	A → C	B → C	C → B	C → A	B → A
Dominant animals	34	0.91	0.09	0.74	0	0	0
Submissive animals	11	0.45	0	0.27	0.09	0.18	0

Twenty-four displays by males clearly acting territorially were taped and analyzed; all had some recognizable components of the signature display. There was however a great deal of variability. Five of seven displays by one male, and four of five by another, were of the signature pattern. The remaining displays for these two animals were varied by having either one or three quick initial bobs instead of two. The third male whose displays were taped had only three of 12 showing the signature pattern. The number of initial bobs (2, 3, or 4), slow bobs (1 or 2), and quick bobs (0, 1, or 2) varied so that for some displays the signature pattern was barely recognizable. The mean number of bobs in these filmed displays was 11.1 ± 0.4. The mean time elapsed was 17.4 ± 0.8 seconds. The coefficients of variation for the number of bobs in these variable units of the signature display in these agonistic encounters are: 24% for the initial bobs, 32% for the slow bob, 40% for the quick bob, and 23% for the total number of bobs in the display. Twenty of these 24 taped displays were accompanied by dewlapping, whereas only 23% of the bobbing displays included dewlap extensions in the total sample of all displays observed. Twenty-two of the taped bobbing displays were two-legged push-ups with crests erected; in 12 displays the body was laterally compressed as well, as the state of arousal during the confrontation increased. Each of the three animals gave one or two displays that began as four-legged push-ups, usually raising the tail on the up stroke of the bob (Fig. 4), and dampened to two-legged push-ups. Tail lifts were used as a modifier of two-legged push-ups in conjunction with nuchal and dorsal crests three times and once with lateral compression as well. One display which included crests and lateral compression also was accompanied by a tongue protrusion and a lip smack.

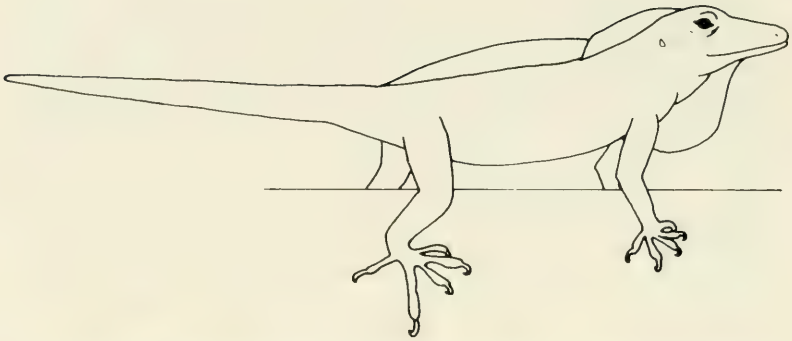


Figure 4. Aggressive display with a 4-legged push-up, nucal and dorsal crests, lateral compression of the body, and a tail lift.

Information on the context of each display type was gained by pooling the data from all the staged encounters in both cage designs and examining the frequency distributions of display types (dewlap flashes, bobbing displays, and bobbing displays with dewlap extensions). Four bobs and dewlap flashes in a continuous sequence were arbitrarily chosen as the minimum to constitute a display. The mean proportion of dewlap fanning displays of all displays was 0.14 $\pm$0.02. There was little intra-individual variation in the proportion of use of this display form from one test to another. In a one-way analysis of variance, 87% of the variation in the frequency of use of this display type was between individuals and 13% between tests of a single individual ($F = 7.28$, $p < 0.01$). This tendency was enhanced by the fact that each male in the cages of Design 1 was always matched against the same opponent and most animals responded in a characteristic fashion in each test. The frequency with which a bobbing display was accompanied by dewlap extension was similarly consistent. Eighty-three percent of the variation was between animals ($F = 4.77$, $p < 0.01$). The mean proportion of bobbing displays with dewlap modifier was 0.23 ± 0.03 (Fig. 5a).

A male was judged to be either submissive or dominant on a test-by-test basis, but he probably performed as both a dominant and submissive individual during the test. Most animals that "lost" ultimately still responded with varying intensity to the challenge of the more aggressive one. In addition, the relative ranks of submission and dominance were not necessarily consistent even

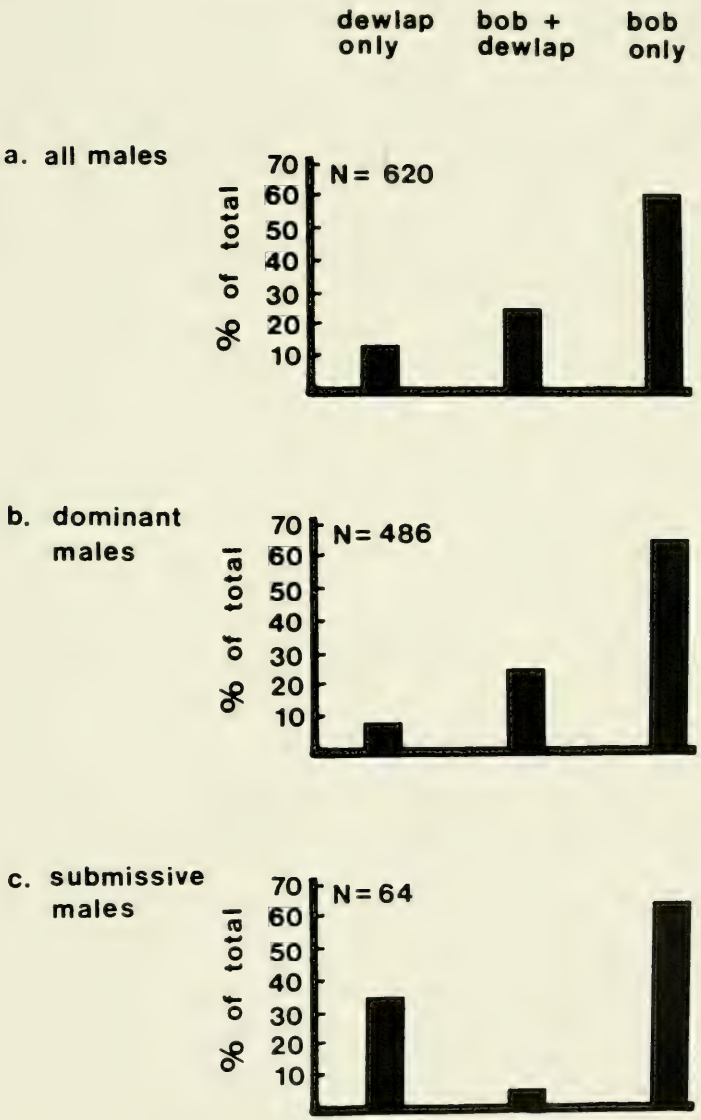


Figure 5. Frequency distribution of display types performed by males in agonistic confrontations. All displays were used in a., but only those by clearly dominant or clearly submissive males were used in b. and c.

when the same opponents were repeatedly matched in the separated aquaria.

Submissive animals displayed (either bobbing or fanning) less than half as often (0.29/minute, N=11) as dominant ones (0.63/minute, N=34) (Table 1). Dewlap fanning formed a significantly higher proportion of the total displays by submissive animals than by dominant animals ($\bar{x} = 0.34 \pm 0.08$ vs. $\bar{x} = 0.08 \pm 0.01$; $t = 2.29$, $p < 0.05$) (Fig. 5b, c). A significantly lower proportion of the bobbing displays of submissive animals was accompanied by dewlap extensions, $\bar{x} = 0.03 \pm 0.01$, than of dominant animals, $\bar{x} = 0.30 \pm 0.03$ ($t = 3.36$, $p < 0.01$). Therefore, submissive animals use their dewlaps for fanning displays but not to modify bobbing displays. A significantly higher proportion of the bobbing displays of submissive animals were the rapid bob (Fig. 3), $\bar{x} = 0.25 \pm 0.09$ for submissive animals versus $\bar{x} = 0.01 \pm 0.01$ for dominant animals ($t = 2.99$, $p < 0.01$). Dominant animals also took progressively more aggressive postures and reached a higher arousal state more frequently than submissive ones did (Table 3).

The pacing of agonistic encounters varies with each fight, even when the combatants are known to each other. Of the pairs that always escalated to a full confrontation, usually the same individual was faster to be aroused. The mean latency time of aggressive animals for developing nuchal and dorsal crests was 4.6 ± 0.4 minutes (N=38) and for lateral compression was 7.4 ± 0.5 minutes (N=26). There was a great deal of intra-individual variation in the kind of displays, if any, that were performed before both crests were erected and the body compressed. But the frequency distribution of display types performed in this low arousal state was different for animals that would be judged dominant or submissive at the end of the test, i.e., there were behavioral differences in the two groups from the beginning of the test (Fig. 6).

A display by one male *A. sagrei* often prompted a display by the other in these tests. Forty percent of all displays seen occurred within 10 seconds after a display or single bob or dewlap flash by the opponent, but there was no particular tendency to use the same sort in answer as the one just seen. For example, a bobbing display was followed by dewlap fanning display or a bobbing display. Forty to 50% of the fanning displays and the bobbing displays with and without dewlap modifier of both dominant and submissive animals was in response to the opponents display. There was a slightly

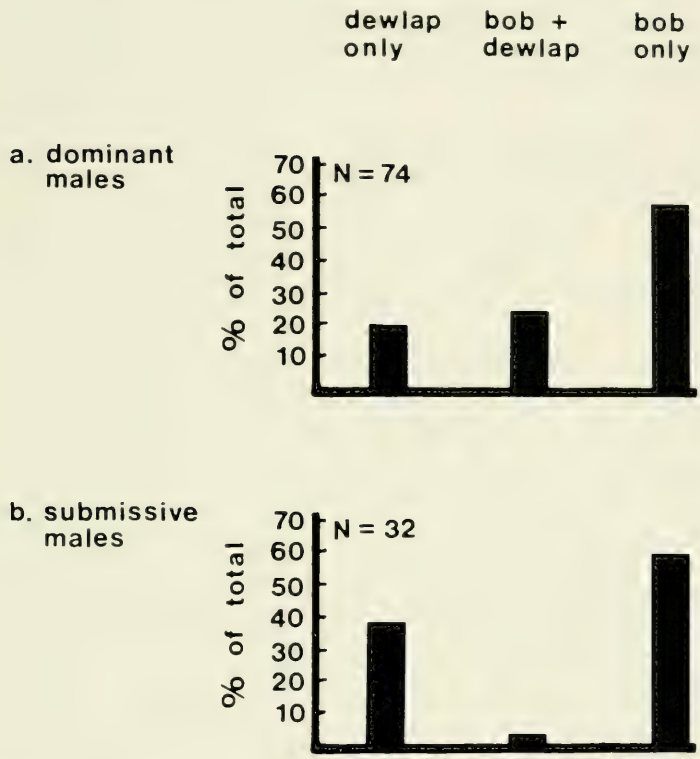


Figure 6. Frequency distribution of display types performed by dominant and submissive animals in agonistic confrontation before nucal or dorsal crests had been erected or the body had been laterally compressed.

higher tendency for a dominant animal to respond with a bobbing display with a dewlap extension. Submissive animals performed almost no bobbing and dewlap displays, but those few that they did perform were all in response to the opponent's display (Table 4).

Male-Female Encounters

All male-female encounters were staged by introducing a female into the wire cage of Design 2 of a single resident male. Eight different males were used in 33 tests. The pattern of courtship behavior appears to be very similar to that described for other anoles (Noble and Bradly, 1933; Evans, 1938; Crews, 1977). Upon

Table 4. Proportion and number of each type of display for submissive and dominant animals which were in response to a display by the opponent rather than spontaneously performed.

	Total displays	Dewlap fanning	Bobbing displays	Bobbing displays + dewlap
Dominant animals	40% (192)	35% (18)	37% (114)	49% (60)
Submissive animals	44% (28)	42% (8)	40% (17)	100% (3)

introduction of a female, the territorial male performs the dewlap fanning display or the bobbing display with or without dewlap extensions either with the signature pattern or not. The bobbing displays seen in a courtship situation have none of the aggressive modifiers, such as crests and lateral compression, that characterize male-male encounters. The male then approaches the female, sometimes with a jiggling action with his head, takes a grip on her neck, and swings his tail beneath hers, juxtaposing his cloaca to hers and inserting a single hemipenis. More displays may follow mating. It has been reported for other anoles (Crews, 1977) that a receptive female will stand and arch her neck for the male to take a grip. In this study, no female was ever seen to show receptive behavior. In all but two of the 33 tests the male attempted to mate by taking or attempting to take a neck grip on the female. Eleven tests ended in copulation. In four of these, the matings were very short (<2 minutes), and the male maintained his mating posture several minutes after the female escaped, indicating that intromission may not have occurred. Excluding those matings which may have been incomplete, the mean time for intromission was 6.7 ± 0.83 minutes.

The anoline courtship display has been characterized as ending with a series of jiggly bobs (Crews, 1975b). In 18 of 33 courtships observed, *A. sagrei* males also performed a jiggle bob at the end of a bobbing display or alone as he approached the female. All eight males performed it in at least one test but only one male always courted using it. When this display was used, it usually immediately preceded an attempted neck grip (15 of 18 tests). This jiggle bob may be an important part of courtship and may be performed with greater regularity if the females showed signs of receptivity.

Of the seven video taped bobbing displays in courtship sequences of three males, only one was the signature pattern. The pattern of the rest could not be characterized. All four displays in the two courtships that ended in neck grips were four-legged push-ups with the tail lifted as the head bobbed up and the dewlap pulsed. This tail lift was a very common (28%) modifier in all courtship bobbing displays.

The overall frequency of all types of displays in courtship sequences by 8 different males in 33 tests was 0.35/minute which is about half that of a dominant male in an agonistic situation (0.66/minute). As was the case of the agonistic tests, the data can be combined because variance of display frequency between performances in different tests was relatively low (0.05). The frequency of bobbing displays with dewlap flashes were similar in premating and postmating displays (0.32 vs. 0.21) which was similar to that in agonistic encounters (0.23). There was both inter- (57%) and intra- (43%) individual variation in the use of the dewlap ($F = 1.3$, $p > 0.20$). The proportion of displays which were dewlap fanning displays were similar in courtship (0.15) and agonistic situations (0.14), but a higher proportion of the displays after mating (0.50) than before (0.10) were dewlap fanning (Fig. 7). Six of the seven complete matings, and none of the short matings, were followed by a dewlap fanning display, most of which had a distinctive erect posture (Fig. 8). But bobbing displays and further attempts to regain a neck grip followed one of the incomplete matings. Thus, bobbing displays may be predominantly a premating signal, and in this context fanning displays may be a signal of a successful copulation.

CONCLUSIONS

The male *Anolis sagrei* of this study show variability in both pattern and contextual use of displays. *Anolis sagrei* has only one species specific stereotypic pattern which may be used in every context. This signature display when used by males in the agonistic encounters was quite variable both in the total number of bobs and the number of bobs in each unit. In addition, the accompaniment of the dewlap extension was also variable; although, if it was used, it was always associated with one particular unit of the display, the

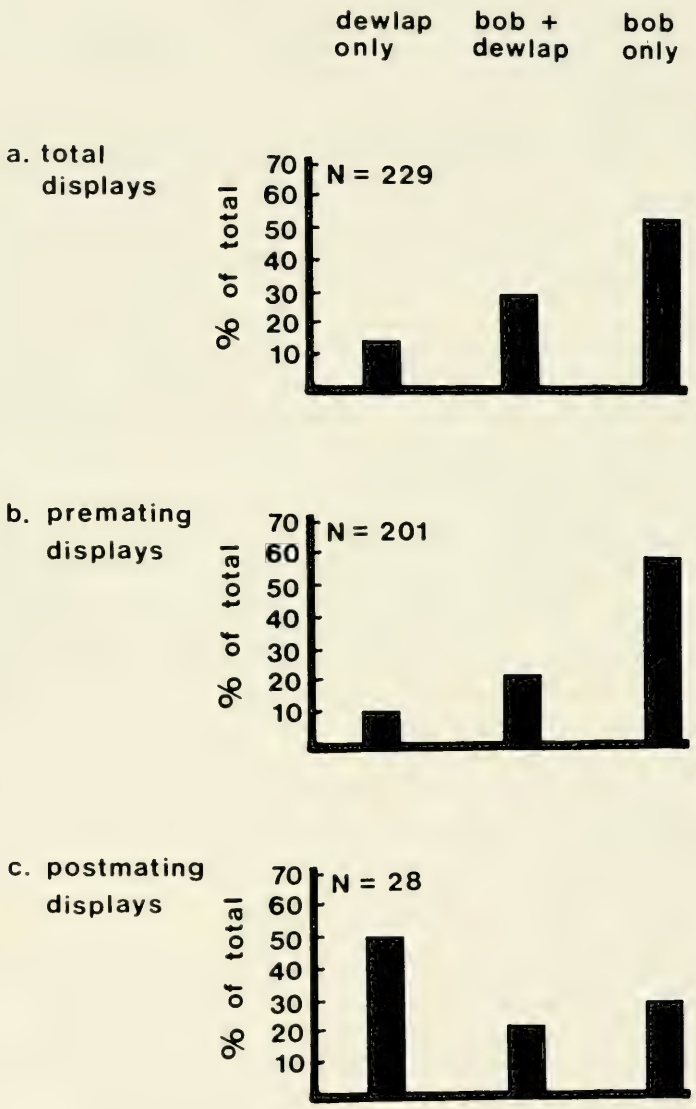


Figure 7. Frequency distribution of display types performed by males in courtship.

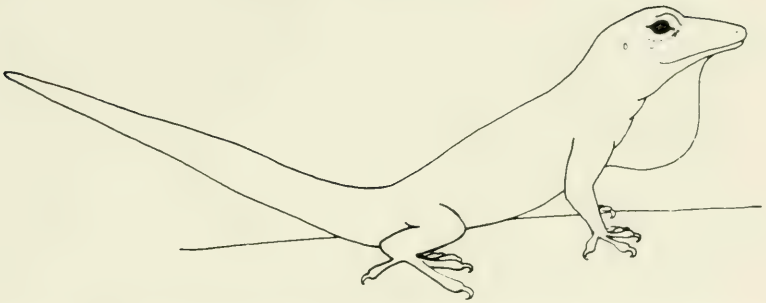


Figure 8. Typical post-copulatory display of dewlap fanning and erect posture.

long bob. This display is so variable that sometimes the signature pattern cannot be recognized. Video taped agonistic and courtship encounters showed that the species-specific signature pattern was used in almost all displays directed toward other territorial males, but was hardly or not at all recognizable in courtship displays.

The only displays which are consistent in their form and use are not species-specific. The jiggle bob, although not always performed in courtships of unreceptive females, was never seen in any other context. The display of rapid rhythmic bobs, shown by submissive males, was not performed by courting males and only rarely by territorial males, and then modified by a very aggressive posture. The dewlap fanning display was seen in all contexts but was used consistently after copulation with a distinct erect posture and may be associated with successful copulation. It has not been described as such for other species, but probably occurs in *A. carolinensis* (Crews, personal communication) and may be used by other anoles.

The color of the dewlap is also a species specific signal. But it may not be a symbol to aid species recognition as much as a means of emphasizing the bobbing display with the bright flash of color (Greenberg and Nobel, 1944; Williams and Rand, 1977). Dominant males in agonistic situations use the dewlap in bobbing displays significantly more than submissive males, but the dewlap is used for fanning displays at a significantly higher frequency by submissive males. Therefore, dewlap flashes alone may be less aggressive signals than when they accompany bobbing displays.

If the dewlap *per se* were being used as a species-specific signal, one might hypothesize an increase in its use in courtship. However,

fanning displays comprise a small proportion of premating displays, which is lower than its average use in other contexts, and the dewlap is used in bobbing displays at only slightly higher frequencies during courtship prior to mating than at other times. Therefore the two signals, the dewlap and the species-specific signature pattern, which one might expect to play a role in species recognition and female choice, are not particularly associated with courship, at least not when the animals are at relatively close range as they were in these tests.

Anolis sagrei originates from Cuba, an island with a very complex *Anolis* fauna (22–28 species, Williams, 1969). The stereotyped display pattern is more variable than one might expect with so many congeneric species needing reproductive isolation (Ruibal, 1967). Information to enable species recognition may be redundantly coded by many physical and behavioral characteristics (Williams and Rand, 1977). This seems to be the case with *A. opalinus* on Jamaica, which has no discrete display pattern even though it is sympatric with its two closest relatives, *A. garmani* and *A. grahami.* All three species have similar dewlap color and display structure but differ greatly in body size, shape, and color (Jenssen, 1979).

The signature display and increased use of the dewlap with the display are associated with territorial status in agonistic encounters. But neither shows an increase in use as the encounter escalates. The state of arousal and the willingness to escalate may be communicated by the modifiers of the displays, especially body posture and shape, and probably by the timing of the events. The more aggressive male of a pair was usually the first to erect his crests, engorge his throat, and laterally compress his body. Small shifts in posture or position in tense moments are probably also used as aggressive signals. Characterization of the behavioral repertoire of *A. sagrei* has been elusive (Ruibal, 1967) because of this subtlety.

ACKNOWLEDGMENTS

I would like to thank E. E. Williams, D. Crews, W. Gartska, T. A. Jenssen, and A. S. Rand for their critical comments on earlier drafts of this paper; J. F. A. Traniello for his technical help and encouragement; B. Scott for the art work; and J. S. Godley for organizing the lizard hunt. This study was supported in part by NIMH Research Scientists Development Award 00135 to D. Crews.

LITERATURE CITED

CARPENTER, C. C. 1967. Aggression and social structure in iguanid lizards, pp. 87–105. *In* W. Milstead (ed.) lizard Ecology: a Symposium, Columbia Univ. Missouri Press.

CARPENTER, C. C., AND G. GRUBITZ. 1961. Time-motion study of a lizard. Ecology **42**: 199–200.

CREWS, D. P. 1975a. Effects of different components of male courtship behavior on environmentally induced ovarian recrudescence and mating preferences in the lizard, *Anolis carolinensis*. Anim. Behav., **23**: 349–356.

_____. 1975b. Inter- and intraindividual variation in display patterns in the lizard, *Anolis carolinensis*. Herpetologica, **31**: 37–47.

_____. 1977. The annotated anole: studies on the control of lizard reproduction. *Am. Sci.*, **65**: 428–436.

EVANS, L. T. 1936. A study of a social hierarchy in the lizard, *Anolis carolinensis*. J. Genet. Psychol., **48**: 88–111.

_____. 1938. Courtship behavior and sexual selection of *Anolis*. J. Comp. Psychol., **26**: 475–497.

GREENBERG, B., AND G. K. NOBLE. 1944. Social behavior of the American chameleon (*Anolis carolinensis* Voight). Physiol. Zool., **17**: 392–439.

GREENBERG, N. 1977. A neurethological study of the display behavior in the lizard, *Anolis carolinensis* (Reptilia, Lacertilia, Iguanidae). Am. Zool., **17**: 191–201.

HOVER, E., AND T. JENSSEN. 1976. Descriptive analysis and social correlates of agonistic displays of *Anolis limifrons* (Sauria: Iguanidae). Behav., **58**: 173–191.

JENSSEN, T. A. 1970a. Female response to filmed displays of *Anolis nebulosus* (Sauria: Iguanidae). Anim. Behav., **18**: 640–647.

_____. 1970b. The ethoecology of *Anolis nebulosus* (Sauria: Iguanidae). J. Herp., **4**: 1–38.

_____. 1971. Display analysis of *Anolis nebulosus* (Sauria: Iguanidae). Copeia, **1971**: 197–209.

_____. 1977. Evolution of anoline lizard display behavior. Amer. Zool., **17**: 203–215

_____. 1978. Display diversity in anoline lizards and problems of interpretation, pp. 269–285. *In* N. Greenberg and P. D. MacLean (eds.) Behavior and Neurology of Lizards, NIMH.

_____. 1979. Display behavior of male *Anolis opalinus* (Sauria, Iguanidae): a case of weak display stereotypy. Anim. Behav., **27**: 173–184.

JENSSEN, T. A., AND E. HOVER. 1976. Display analysis of the signature display of *Anolis limifrons* (Sauria: Iguanidae). Behav., **57**: 227–240.

JENSSEN, T. A., AND L. M. ROTHBLUM. 1977. Display repertoire analysis of *Anolis townsendi* (Sauria: Iguanidae) from Cocos Island. Copeia, **1977**: 103–109.

NOBLE, G. K., AND H. T. BRADLEY. 1933. The mating behavior of lizards: its bearing on the theory of sexual selection. Ann. N. Y. Acad. Sci., **35**: 25–100.

RAND, A. S., AND E. E. WILLIAMS. 1970. An estimate of redundancy and information content of anole dewlaps. Am. Natur., **104**: 99–103.

RUIBAL, R. 1967. Evolution and behavior in West Indian anoles, pp. 116–140. *In* W. W. Milstead (ed.), Lizard Ecology: a Symposium, Columbia Univ. Missouri Press.

STAMPS, J., AND G. BARLOW. 1973. Variation and stereotypy in the displays of *Anolis aeneus* (Sauria: Iguanidae). Behav., **48**: 67–94.

WILLIAMS, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. Quart. Rev. Biol., **44**: 345–389.

———. 1976. West Indian Anoles: a taxonomic and evolutionary summary. I. Introduction and species list. Breviora Mus. Comp. Zool. No. 440, pp. 1–21.

WILLIAMS, E. E., AND A. S. RAND. 1977. Species recognition, dewlap function and faunal size. Am. Zool., **17**: 265–274.

MUS. COMP. ZOOL
LIBRARY
JUN 17 1985
HARVARD
UNIVERSITY

BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 21 JUNE 1985 NUMBER 480

THREE NEW LIZARDS OF THE GENUS *EMOIA* (SCINCIDAE) FROM SOUTHERN NEW GUINEA

WALTER C. BROWN[1] AND FRED PARKER[2]

ABSTRACT. Three new species of skinks in the genus *Emoia* are described from provinces south of the central mountain range, New Guinea.

INTRODUCTION

The genus *Emoia* is widespread through much of the Indo-Australian Archipelago and the islands of the Pacific, and ranges into the Philippines in the north and northeastern Australia and New Hebrides in the south. The greatest diversity of species occurs in New Guinea and surrounding smaller islands. The three new species described in this paper are from south of the central mountain range in New Guinea.

One species is based on a series of specimens collected primarily by the junior author in the Fly River and Bamu River drainages, Western Province, Papua New Guinea. The second ranges from Western Province westward through southern Irian Jaya. Both species are in the E. *baudini-submetallica* group as defined by Brown, 1953. The third species which belongs to the *E. physicae* group (Brown, 1953) has a wide range in several provinces of southern Papua New Guinea. The last two, in addition to the series collected by the junior author, are also represented in earlier collections.

[1]Department of Herpetology, California Academy of Sciences, San Francisco, California 94118, and, Menlo College, Menlo Park, California 94025.
[2]717 Ross River Road, Kirwan, Queensland, Australia.

These had been misidentified as juveniles of *E. p. physicae, E. p. tropidolepis*, or *E. baudini*.

Emoia aurulenta new species
(Fig. 1)

Holotype: MCZ 142327, adult male, collected at Migalsimbip in the upper Fly River drainage at an elevation of about 1,200 m, Western Province, Papua New Guinea, Fred Parker Coll., 16 August 1972.

Paratypes: The following localities in Western Province, Papua New Guinea, Migalsimbip: SAM 11637; AM 40778; MCZ 142322–26, 142328–30, 152268–71, 152273–75, CAS 154186, AMNH 111718; UPNG 6477–78, 6480, 6483; Derongo: MCZ 131895–900; AMNH 103961; Menemsore: MCZ 131901; Emeti: MCZ 152265–67, 152291, AMNH 111715; Tingkem: MCZ 131894.

Diagnosis. This species differs from the other New Guinean species of the *Emoia baudini* section in the following combination of characters: (1) small size, 37+ to 49.5 mm snout-vent length at maturity; (2) pattern of gold-orange markings on the sides of the neck and the lateral surfaces of the body in life (these fade to dirty, silvery-white in preservative); (3) low number of midbody scale rows; 26 to 32 (mean 28+), rarely greater than 30; (4) number of subdigital lamellae, 39 to 48 beneath the fourth toe; and (5) number of paravertebral scale rows between the parietals and base of tail 45 to 52.

Description. A small *Emoia*, snout-vent length of 41.3 to 49.5 mm for 16 males and 37.4 to 47.5 mm for eight females; habitus moderately slender; snout moderately tapered, bluntly rounded, its length 35 to 40% of head length and 52 to 60% of head breadth; head breadth 64 to 69% of head length and 15 to 18% of snout-vent length; eye moderately large, its diameter 71 to 85% of snout length and 40 to 45% of head breadth; ear diameter about one third to one half of eye diameter; rostral broader than high, forming long, nearly straight suture with frontonasal; supranasals widely separated, narrowly triangular, in contact with anterior loreal; prefrontals moderately to widely separated; frontal longer than broad, rounded posteriorly, shorter than fused fronto-interparietal shield, in contact with first and second supraoculars; four large supraoculars; parietals large, in contact posteriorly; one pair of nuchals; anterior

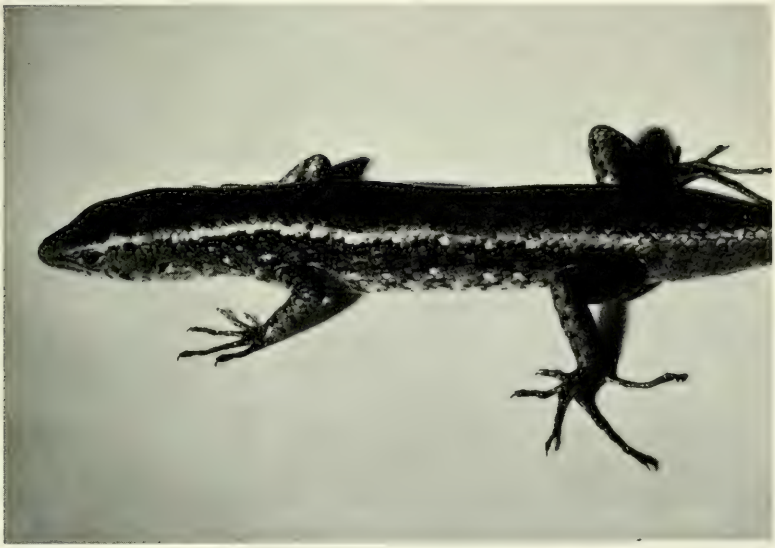


Figure 1. An adult *E. aurulenta*.

loreal higher and shorter than posterior, in contact with second, or first and second supralabials; six to seven upper labials, fifth (very rarely sixth) enlarged and beneath eye; six to seven lower labials; dorsal scales smooth, vertebral rows not distinctly enlarged; 26 to 32 (usually 28 to 30) midbody scale rows; 45 to 52 (mean 48.3) paravertebral rows between parietals and base of tail, ventrals about same size as dorsals; preanals somewhat enlarged; limbs well developed, length of extended hind limb 90 to 110% of axilla-groin distance and 47 to 54% of snout-vent length; 39 to 48 (mean 42.6) smooth, rounded lamellae beneath fourth toe; 10 to 14 lamellae under first toe; rank of adpressed toes from longest to shortest four, three, two to five, one; tail slender and much longer than body.

Measurements (in mm) of Holotype. Snout-vent length 49.0; axilla-groin distance 24.8; hind limb length 24.1; head length 11.9; head breadth 8.1; snout length 4.35; eye diameter 3.4; ear diameter 1.5; tail length 76.4.

Color in Preservative. The basic ground color on the dorsum ranges from light olive greenish-brown to brown marked by lighter and darker blotches, usually involving all dorsal scale rows (or occasionally not including the paravertebral rows). The light and dark

blotches may occupy alternate scales or involve two or more scales. The upper lateral surfaces are dark brown, bordered dorsally by a row of scattered, single or clustered, pale scales. There are also scattered pale scales between and on the limbs. The neck is marked by pale and dark blotches, and the posterior labials by dark bars. The venter is dirty white to grayish, lightest on the chin and in the limb regions.

In life, the top of the head is bronze with a lighter line from above the eye to the nuchals or for a few specimens extending further posterior onto the neck. The dorsum is gray or brown with alternate black scales or paravertebral rows of black spots in a checkerboard pattern. The upper flanks are black or mottled black and brown. The lower flanks and usually the side of the neck are marked by golden yellow spots. The venter is yellowish to cream.

Comparison. Emoia aurulenta is related to Papuan species of the *E. baudini-submetallica* group, but is readily distinguished in life by such features of the color pattern as the checker-board pattern on the dorsum and the prominent golden yellow spots on the sides. It also is characterized by a lower number of midbody scale rows than other known species of this section. Also, the number of subdigital lamellae is greater than for most other species of this group, only overlapping slightly with *E. s. popei* and two other undescribed species (Table 1).

Etymology. The name *aurulenta* refers to the golden yellow spots on the sides.

Note on Reproduction. No data are available for this species.

Note on Habitat. This is a diurnal species which is active on the rain forest floor beneath the unbroken canopy.

Range. Emoia aurulenta is known only from the Fly and Bamu River drainages in the Western Province, Papua New Guinea.

Another undescribed species represented by samples from several populations south of the central mountain range between Western Province in Papua New Guinea and the Jamur Lake area in western Irian Jaya can not be identified with any previously described species of *Emoia*. Four specimens from various localities in Western Province, Papua New Guinea were collected by Fred Parker in 1969 and 1971. A series of specimens in the Leiden Museum collected during a 1955 survey and the 1959 expedition along the Digul River and several of its tributaries in southeast Irian Jaya and several collected earlier at more westerly locations (identified as *E.*

baudini) also belong to this species. These were collected in part by the British Ornithological Expedition in the Mimika River area in 1913 and in part by the Royal Netherlands Geographical Society Expedition in the Jamur Lake area in 1959.

Emoia aenea new species
(Fig. 2)

Lygosoma baudini, (part) Boulenger, 1914, Trans. Zool. Soc. London, **20:** 259.

Holotype: MCZ 131949, adult male, collected at Menemsore, Western Province, Papua New Guinea, Fred Parker coll., 30 March 1969.

Paratypes: The following localities in Western Province, Papua New Guinea, Matkomrae: MCZ 144393, Emeti: MCZ 144386, Kiunga: MCZ 131948; the following localities in Irian Jaya, Mimika River area: BMNH 1913.11.1.81–82, 1913.10.31.164F; Gariau, Jamur Lake area: RMHN 21278; lower Digul River, Tanah Merah: RMHN 21180–85, 21273–74, 21276–77; 21279; Tanah Tinggih: RMHN 21275, 21280–82; Kouh: RMHN 21186–89; CAS 156680; Mariang: RMHN 21190–94.

Figure 2. An adult *E. aenea*.

Table 1. Pertinent scale counts and measurements of the species of *Emoia* described in this paper and related species.

Species	Number in sample	Snout-vent length adults (in mm)	Keels on scales		Upper labial beneath eye		Midbody scale rows	Scale rows between parietals and tail	Fourth toe lamellae
			present	absent	5th	6th			
E. aurulenta new sp.	28	37.0–49.5		x	20		R=26–32	R=45–52	R=39–48
E. aenea new sp.	27	53.5–71.0		x	3	15	R=31–36	R=49–54	R=39–46
E. s. popei	29	44.9–65.0		x	5	21	R=34–42	R=44–52	R=37–44
E. s. obscura	75	43.9–63.5		x	68	9	R=30–39	R=43–55	R=30–41
E. physicina new sp.	38	39.0–50.4	x		25	2	R=30–38	R=45–54	R=34–43
E. physicae	108	48.9–74.3	x		11	92	R=34–43	R=45–58	R=32–42

Diagnosis. This species can be differentiated from other species of the *E. submetallica* complex on the basis of the following combination of characters: (1) 31 to 36 midbody scale rows; (2) 49 to 54 paravertebral scale rows between the parietals and the base of the tail; (3) 39 to 46 rounded lamellae under the fourth toe; (4) sixth (rarely fifth) upper labial enlarged and beneath the eye; (5) snout-vent length at maturity 53.5 to 71.0 mm; (6) such features of the color pattern as dorsum medium brown (in life bronzy anteriorly), sometimes with darker blotches in longitudinal series mostly lateral to the paravertebral scale rows; upper lateral surfaces (two or three rows of scales) darker brown to blackish, lower lateral surfaces grayish slate; venter whitish to ivory, occasionally more grayish on head and abdominal regions, pale spot on neck absent.

Description. An *Emoia* of intermediate size, snout-vent length 53.5 to 71.8 mm for 11 males and 59.6 to 69.5 mm for three females; habitus moderately robust, limbs well developed; snout moderately tapered, bluntly rounded, its length 54 to 62% of head breadth and 34 to 39% of head length; head breadth 58 to 69% (rarely less than 60%) of head length and 14 to 17% of snout-vent length; eye relatively large, its diameter 67 to 90% of snout length and 36 to 50% of head breadth; ear diameter one quarter to nearly one half of eye diameter; rostral broader than high, forming long, nearly straight suture with frontonasal; supranasals narrow, elongate, in contact with anterior loreal; prefrontals moderately to widely separated; frontal longer than wide, about same length as fused fronto-interparietal shield, broadly rounded posteriorly, in contact with first and second supraoculars; four large supraoculars; seven or eight supraciliaries; parietals large, in broad contact posteriorly; one pair of nuchals; anterior loreal shorter and higher than posterior, in contact with first and second, second, or second and third upper labials; usually six to eight upper labials, sixth (occasionally fifth) enlarged and beneath eye; seven or eight lower labials; dorsal scales smooth, paravertebral scales not or scarcely enlarged; midbody scale rows 31 to 36; paravertebral scale rows between parietals and base of tail 49 to 54; preanals not or slightly enlarged; limbs well developed, length of extended hind limb 91 to 120% of axilla-groin distance and 45 to 54% of snout-vent length; 39 to 46 rounded lamellae under fourth toe; 10 to 14 lamellae under first toe; rank of adpressed toes from longest to shortest four, three, two, five, one; tail longer than body.

Measurement (in mm) of Holotype. Snout-vent length 71.0; axilla-groin distance 34.7; hind limb length 31.7; head length 17.8; head breadth 10.0; snout length 6.2; eye diameter 5.7; ear diameter 1.5; tail length 104±.

Color in Preservative. The dorsal ground color ranges from tan to a vaguely grayish-brown or a light brown. It may be nearly uniform or be marked by a longitudinal row of dark brown blotches or sometimes dark brown, narrow, marginal lines on the scale rows lying lateral to the paravertebral rows. The top of the head, except sometimes the margins of the scales is relatively uniform. The upper lateral surface is marked by a narrow, darker brown band varying from one or two to three or four scale rows in breadth, narrowing on the neck and head and scarcely evident on the snout. This band is sometimes bordered by scattered, pale scales along its dorsal margin and there are numerous pale scales on the lower lateral surfaces, but the dark band itself it usually unmarked. The upper part of the upper labials are dusky, and there are some dark marks on some of the lower labials. The venter is whitish ivory, unmarked, and the undersurface of the tail has scattered, small, blackish or grayish spots.

In life the head and neck are bronzy, the belly white. The Kiunga specimen has a patch of pink just anterior to the vent, the Menemsore specimen a patch of orange. The dorsal scales are smooth and iridescent.

Etymology. The name *aenea* refers to the bronzy coloration on the top of the head and anterior body.

Comparisons. This species is close to *E. submetallica obscura* and *E. submetallica popei* in scale counts. In color *E. aenea* is more similar to *E. s. obscura* than to *E. s. popei*, lacking the small, whitish blotch on the side of the neck which is typical of the latter. *E. aenea* also appears to be slightly larger in size and the number of subdigital lamellae may be slightly greater than for either of the two subspecies of *submetallica* (Table 1), although it is closest to *E. s. popei* in this character. Also the sixth upper labial is usually the one which is enlarged and beneath the eye for *E. s. popei* and *E. aenea*, whereas it is the fifth for *E. s. obscura*.

Note on Reproduction. RMHN 21281, a gravid female measuring 62.2 mm snout-vent length, has two eggs in the oviducts.

Habitat Note. Parker's specimens were found in primary forest in areas of high rainfall. All localities are at low elevation between sea level and 100 m.

Range. Known from Western Province, Papua New Guinea, and Mimika River, Digul River and Jamur Lake areas in southern Irian Jaya.

Emoia physicina new species
(Fig. 3)

Holotype. MCZ 152287, adult male, collected near Emeti, Western Province, Papua New Guinea at an altitude of about 100 m, Fred Parker coll., October 1971.

Paratypes. Same locality as holotype: MCZ 142567–72, 152283–86, 152288, 152290, AMNH 111713–14; other localities in Western Province, Menemsore: MCZ 131945–46, 152280; Kiunga: MCZ 152281–82; Derongo: AMNH 111712, MCZ 131938–39, 131942; Matkomrae: MCZ 131943–44; localities in other provinces of Papua New Guinea, Chimbu Province, Karimui: MCZ 97308–09, 99193–96, 109579–82, 109584–96, CAS 117731, 117750, 118769–70, 118807; Soliabeda: CAS 117733–34, MCZ 109509, 109589–96, 109598–99; Dege: MCZ 90750; Bomai: MCZ 90478–501; Eastern Highlands Province; AMNH 98570a–b; Gulf Province, Pio River: AMNH 102233, CAS 118871–72; MCZ 109601–03; Koni: CAS 117726–27; MCZ 109514, 109529, 109532; Uraru: CAS 117753–54, MCZ 109572–75, 109577– 78; Oroi: MCZ 109833; Weiana: MCZ 109521–23; localities in Irian Jaya, Assike on the Digul River: RMHN 5081a–b.

Diagnosis. This species can be distinguished by the following combination of characters: (1) relatively weak keels on the dorsal scales, especially on the posterior half of the body; (2) small size, 39.0 to 50.7 mm snout-vent length; (3) relatively low midbody scale count 30 to 38; (4) fifth upper labial enlarged and beneath the eye; (5) number of vertebral scale rows between the parietals and base of tail 45 to 54, and (6) number of fourth toe lamellae 34 to 43.

Description. A relatively small *Emoia*, snout-vent length 39.0 to 50.7 mm for twelve mature males and 43.3 to 50.0 mm for fourteen mature females; habitus moderately slender with well-developed limbs; snout moderately tapered, broadly rounded at tip, its length

Figure 3. An adult *E. physicina*.

51 to 60% of head breadth and 35 to 39% of head length; head breadth 60 to 72% of head length and 15 to 18% of snout-vent length; eye relatively large, its diameter 72 to 85% of snout length and 39 to 46% of head breadth; ear moderate, its diameter about two fifths to three fifths of eye diameter, usually with two lobules anteriorly; rostral broader than high, forming long, convex or truncate suture with frontonasal; prefrontals moderately to widely separated; frontal slightly longer than broad, about as long as fronto-interparietal shield, in contact with two anterior supraoculars; four large supraoculars; frontoparietals fused with interparietal into one shield; parietals in contact; one pair of nuchals; anterior loreal shorter and slightly higher than posterior loreal, in contact with first or first and second upper labials; seven or eight upper labials, fifth (very rarely sixth) enlarged and beneath eye; six or seven lower labials; dorsal scales, at least posteriorly, with three weak to moderate keels; 30 to 38 scale rows at midbody; 45 to 54 (rarely greater than 53) paravertebral rows between parietals and base of tail; limbs well developed, length of extended hind limb 91 to 105% of axilla-groin distance and 44 to 54% of snout-vent length; 34 to 43 rounded lamellae beneath fourth toe (only one specimen has

more than 40); 8 to 10 beneath first toe; rank of adpressed toes from longest to shortest four, three, five, two, one; tail much longer than body.

Measurements (in mm) of Holotype. Snout-vent length 48.1; axilla-groin distance 21.9; hind limb length 22.6; head length 12.9; head breadth 8.3; snout length 4.5; eye diameter 3.4; ear diameter 1.6; tail length 74.8.

Color in Preservative. The dorsum (six to eight scale rows) is medium brown, nearly uniform or with rows of darker brown spots marginal to the paravertebral rows. The lateral surfaces, at least five to six upper scale rows, are usually much darker brown, nearly uniform or with scattered single or small groups of pale or whitish scales and often one or two light scales on neck. The upper labials are dusky, at least on the dorsal half, and the lower labials may or may not have dusky blotches. The venter is grayish slate, more dusky tan or ivory in the limb region.

For living specimens, the dorsum is grayish-brown to brown, usually with two rows of paravertebral dark spots. Lateral surfaces are blackish with scattered light spots on the lower flanks. Some specimens have the upper and lower surfaces of the snout suffused with red.

Etymology. The name *physicina* refers to the fact that the species has been confused with juveniles of other keel-scaled species such as *E. physicae.*

Comparisons. Emoia physicina can be distinguished from all other known species of the *E. physicae* section except *E. callistica* (1) on the basis of its small size, (2) the very weak keels which separate it from all but *E. kuekenthali*, (3) in having the fifth instead of sixth upper labial enlarged and beneath the eye. It differs from *E. callistica* in lower number of midbody scale rows and subdigital lamellae, in the distinct nuchals, and in the very weak rather than strong keels on the dorsal scales.

Note on Reproduction. Gravid females CAS 110360, 49.3 mm snout-vent length and CAS 118770, 50.0 mm snout-vent length have two eggs in the oviducts. One hatchling (MCZ 90750) measures 24 mm snout-vent length.

Habitat Note. This species occupies the rain forest floor in areas shaded by the canopy. Specimens do bask in sunflecked areas, however. It is strictly diurnal.

Range. E. physicina is known from the following provinces in southern Papua New Guinea: Eastern Highlands, Gulf, Chimbu, and Western.

ACKNOWLEDGMENTS

We wish to thank Pere Alberch and Ernest E. Williams, Museum of Comparative Zoology (MCZ), Allen E. Greer, Australian Museum (AM), Richard G. Zweifel, American Museum of Natural History (AMNH), John Pernetta, University of Papua New Guinea (UPNG), R. C. Drews and A. E. Leviton, California Academy of Sciences, and Terry D. Schawner, South Australian Museum (SAM) for the loan of material used in this study. The senior author also thanks the trustees of the Australian Museum and the Science and Industry Endowment Fund, Commonwealth Scientific and Industrial Research Organization of Australia, for their financial assistance while studying in the museums of Australia. Robert Drewes and Allen Greer have read the manuscript and been most helpful with their suggestions.

LITERATURE CITED

Brown, W. C. 1953. Results of the Archbold Expeditions No. 69. A review of New Guinea lizards allied to *Emoia baudini* and *Emoia physicae*. Amer. Mus. Novitates, No. 1627, pp. 1–25.

MUS. COMP. ZOOL
LIBRARY
JUN 17 1985
HARVARD UNIVERSITY

B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 21 JUNE 1985 NUMBER 481

A NEW *ANOLIS* OF THE *LIONOTUS* GROUP FROM NORTHWESTERN ECUADOR AND SOUTHWESTERN COLOMBIA (SAURIA: IGUANIDAE)

KENNETH MIYATA[1]

ABSTRACT. *Anolis lynchi*, new species, is described from several lowland rain forest localitites in northwestern Ecuador and southwestern Colombia. It is allied to the semiaquatic anoles of the *lionotus* species group, and appears to be most closely related to *Anolis poecilopus* Cope of Panama and northwestern Colombia. The *lionotus* species group and the known distribution of its South American representatives is discussed.

INTRODUCTION

Much of the complexity of the South American *Anolis* fauna is contained within the narrow confines of the wet Pacific coastal region of Colombia and Ecuador (see Table 2 in Williams, 1976). Although these anole communities may be richer than similar Amazonian communities (up to perhaps twelve sympatric species vs. six in Amazonia), a major feature of the region seems to be more restricted ranges of the individual species and narrower microhabitat preferences. Localities close together geographically may have strikingly different faunas, and within a single fauna there may be distinct forest and forest edge components.

Until recently there were few representative series of most South American anoles. Moderate to large series of some species from the Andes and their western and eastern flanks have been collected

[1]Deceased; formerly Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

during the past decade by workers interested primarily in frogs, who find sleeping anoles at night. These have sometimes been the ones most poorly represented in museum collections; in some cases it seems as if a different anole fauna can be found at night. Field parties from the University of Kansas led by Dr. John D. Lynch have night-collected a series of anoles from the vicinity of Santo Domingo de los Colorados, Provincia del Pichincha, Ecuador. Some of these prove to represent a new species, which I here name:

Anolis lynchi, new species
(Figs. 1–4)

Holotype: MCZ 124406, an adult male from Santo Domingo de los Colorados, 600 m elevation, Provincia del Pichincha, Ecuador, R. W. Henderson coll., 31 July 1968.

Paratypes: ECUADOR: *Provincia del Pichincha:* KU 178953, Santo Domingo de los Colorados, 580 m, elevation J. D. Lynch coll., 12 June 1977; KU 178954-178958, 2 km E, 1 km S Santo Domingo de los Colorados, 600 m elevation, T. Berger and J. D. Lynch coll., 13 June 1977, and KU 178959 from the same locality, J. D. Lynch coll., 11 July 1977; MCZ 157156, 2 km E, 1 km N Santo Domingo de los Colorados, 620 m elevation, J. D. Lynch coll., 31 July 1977; *Provincia de Esmeraldas:* USNM 211222, 1–2 km W El Placer, 390–410 m elevation, J. A. Peters coll., 1 December 1958.

Refered specimens: COLOMBIA: *Departmento del Cauca:* AMNH 107864-70, 109598-602, Quebrada Guangui, 0.5 km above Río Patía, upper Saija drainage, 100–200 m elevation.

Diagnosis. Anolis lynchi can be distinguished from all other known species of South American *Anolis* by the high number of scales across the snout (18–29 at level of second canthals), the small, subequal scales in the supraocular area, distinct pale flank stripes, and the greatly enlarged bilobed hemipenes of adult males.

Description. Head. Head scales small, flat to slightly granular. (Counts for holotype are in parentheses.) Eighteen to 29 (28) scales across snout at level of second canthals. Seven to 10 (8) scales border rostral posteriorly. Circumnasal scale separated from rostral by one to two (2) scales. Nine to 12 (10) scales between supranasals. Supraorbital semicircles distinct, raised, separated medially by three to six (4) scales. Supraocular scales small, subequal, slightly

Figure 1. *Anolis lynchi*, new species. Illustration based on Kodachrome slide of KU 178953, an adult male paratype from Santo Domingo de los Colorados, Provincia Pichincha, Ecuador.

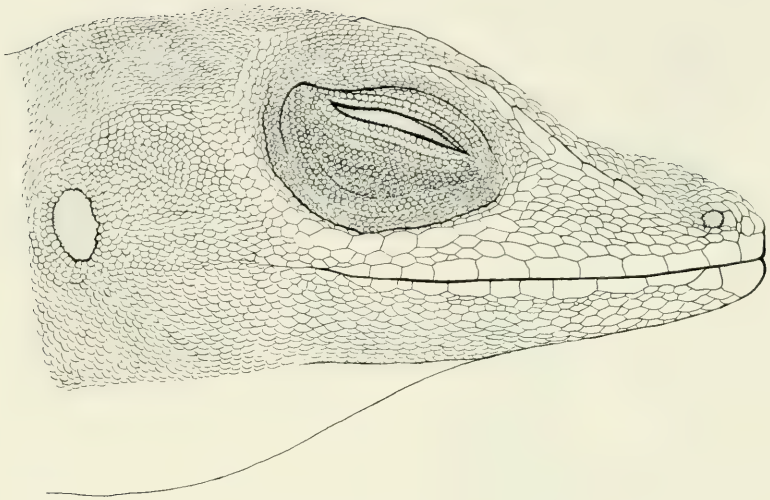


Figure 2. *Anolis lynchi*, new species. Lateral view of head of holotype (MCZ 124406).

keeled to granular, 11 to 19 (18) across widest point. Supraciliaries three to five (4). Canthus distinct in adults, less so in juveniles; five to six (5) canthals, the second the largest. Loreal rows seven to ten (10), subequal. Nasal area slightly swollen in adults.

Temporals and intertemporals granular. Interparietal slightly smaller than ear opening, separated from supraorbital semicircles by four to six (4) scales. Interparietal much smaller than ear opening in some specimens. Scales anterior to interparietal enlarged or subequal (enlarged) with respect to temporals; scales posterior to interparietal slightly flattened or granular (flattened), larger than, but grading into, dorsal scales. No enlarged supratemporal rows. Distinct thin fold extending from supraorbital semicircles laterally to mid-orbit, where it extends posteriorly above ear opening and fades out in axillary region.

Suboculars slightly keeled, separated from supralabials by one row of scales. Seven to 10 (10) supralabials to center of orbit.

Mental groove extending approximately three quarters across, each part much wider than deep. Six to eight (7) scales in contact with mental posteriorly. Eight to 11 (11) infralabials. Chin scales granular, except for some which are slightly keeled.

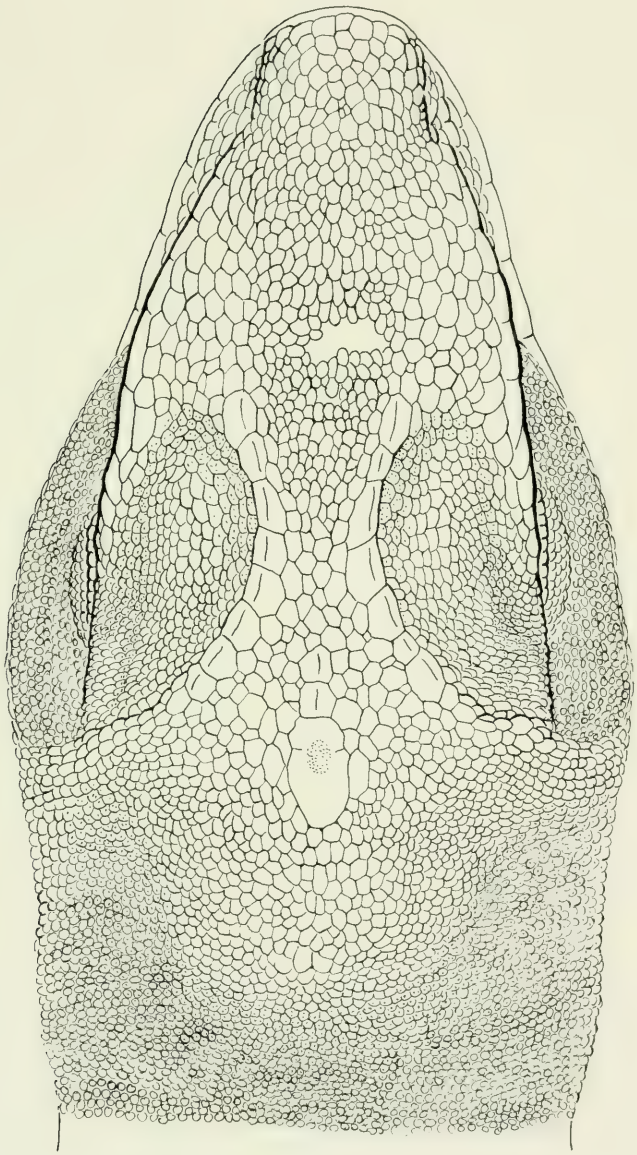


Figure 3. *Anolis lynchi*, new species. Dorsal view of head of holotype (MCZ 124406).

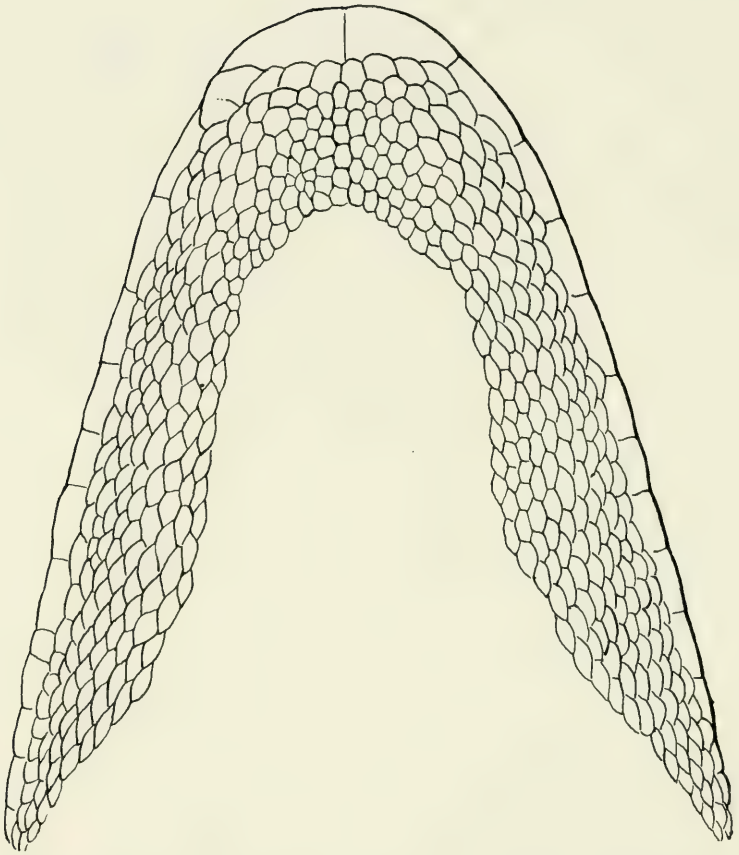


Figure 4. *Anolis lynchi*, new species. Ventral view of head of holotype (MCZ 124406).

Dewlap. Dewlap of adult males medium-size, extending from under the midpoint of the orbit posteriorly to a point just under the axilla. Scales form 13 to 16 longitudinal rows when dewlap extended, but arranged irregularly and not parallel. Dewlap scales narrowly compressed laterally and elongate, especially at the edge. Dewlap of adult females small.

Trunk. Middorsal scales flattened or slightly keeled (flat); two medial rows slightly larger than adjoining rows. Lateral scales granular, grading into larger, subimbricate ventral scales. Ventral scales

slightly to moderately keeled; keeling more prominent midventrally than anteriorly or posteriorly.

Limbs and Digits. Scales on limbs smooth to lightly keeled; generally smoother on upper arm and thigh than on lower arm or calf. Scales on forearm subequal; those on hind limbs are larger anteriorly. Keeling on limb scales unicarinate. Supradigital scales multicarinate, usually with two longitudinal keels. Fifteen to 18 (17) lamellae under phalanges ii and iii of fourth tow. Distal phalanx raised slightly above adjacent phalanx.

Tail. Base of tail greatly swollen in adult males, slightly thicker than trunk in pelvic region, tapering abruptly about one quarter SVL behind the vent. Tail slightly compressed laterally, height about 20 percent more than width. Caudal scales unicarinate, more strongly keeled ventrally than laterally or dorsally. Males with a distinctly keeled middorsal scale row beginning where the swollen tail base ends. Postanals not enlarged.

Hemipenes. The hemipenes of adult males are greatly enlarged, accounting for the extreme swelling at the base of the tail. The everted hemipenes are bifurcate, the split extending back about one third of the distance from the distal end to the base. The distal end has small calyces that become larger proximally. The shaft has large folds, becoming smoother on the base. The sulcus spermaticus has several longitudinal folds.

Measurements. Adult males 54.2 to 61.8 mm snout-vent length (SVL), adult females 49.5 to 59.3 mm SVL.

Color as Preserved. The dorsum ranges from cinnamon-brown to deep fuscous. Males show indistinct lighter brown longitudinal stripes dorsolaterally; females have a distinct gray middorsal stripe. Some males show a broken and indistinct series of small, elongate dark brown marks middorsally. Both sexes show traces of indistinct pale and dark brown lateral stripes that are very thin just above a prominent muddy gray flank stripe. The gray is heavily flecked with brown, but the flank stripes are very distinct in most specimens. Below this flank stripe is a dark brown stripe heavily flecked with gray. The gray flank stripe extends to the orbit, and the sides of the head are gray with brown flecks and spots. The venter is an almost immaculate light gray to cream, with some gray flecking laterally. The undersides of the limbs and tail are lightly mottled with brown.

Color in Life. The following description of Ecuadorian speci-

mens from Santo Domingo de los Colorados is compiled from the field notes and Kodachrome transparencies of living animals provided by John D. Lynch.

The dorsum is brown to reddish brown, with an obscure series of dark brown middorsal blotches in males and a pale gray middorsal stripe in females. The flank stripe is dull cream and is bordered above by a thin, yellowish cream stripe. The flanks are mottled brown, with an olive wash in some specimens. The sides of the head are off-white with dark brown marks under the orbits. The chin, venter, and underside of the limbs are cream; the underside of the tail of females and the underside of the tail of males posterior to the swollen tail base is yellowish. The dewlap is orange with white scales. The iris is bright coppery brown. The tip of the tongue is gray.

Color notes of the Colombian specimens were provided by Charles W. Myers. They were similar to the Ecuadorian specimens, except Myers noted grayish chins, a dull gray reticulum under the limbs, and the dewlaps were *dull* orange (Myers' italics). Myers also noted that the throat lining was unpigmented.

Etymology. The species is named after John D. Lynch, whose indefatigable excursions into the Ecuadorian night are responsible for many of the known specimens.

Variation. The Colombian specimens referred to *Anolis lynchi* differ somewhat from the Ecuadorian sample. They have fewer scales across the snout at the second canthals (18–24 vs. 25–29) and fewer scales across the supraocular region (11–15 vs. 15–18). Both counts reflect slightly larger head scales in the northern population. There also appears to be a slight difference in color of living animals. The Ecuadorian specimens had immaculate cream venters while those of the Colombian specimens were cream with a dull gray reticulum under the limbs and a grayish throat. The dewlaps of adult males from both areas were basically orange, but those of the northern population were characterized as a dull orange while those of the southern populations were a fairly bright orange.

Despite the differences seen between the Ecuadorian and Colombian populations, I regard them as conspecific. The differences may well be clinal, and there is no evidence for sharp discontinuities in character states that might reflect breaks in gene flow. However, since there is a possibility that the Colombian populations may be distinct, I have not designated these specimens as paratypes.

Comparisons. *Anolis lynchi* most closely resembles *A. poecilopus* of Panama and northwestern Colombia. The two are closely related (see discussion below), but can be distinguished by the characters summarized in Table 1.

The reduced supraocular scales of *A. lynchi* are paralleled in two other groups of South American anoles. The *latifrons* group includes several giant anoles with adult SVLs of 125 mm and more. The *aequatorialis* group is a poorly known complex of medium to larger size anoles (adult SVLs generally over 80 mm). Species in both groups lack transverse processes on the posterior caudal vertebrae and are alpha anoles in the terminology of Etheridge (1960). Since *Anolis lynchi* has these transverse processes, it falls into the beta section of the genus. *Anolis lynchi* can be easily distinguished from any known member of the *latifrons* or *aequatorialis* groups by its smaller adult size (less than 65 mm SVL vs. 80 mm or more), much smaller supraocular scales (11–19 across), smaller scales across the snout (at least 18 at level of second canthals), and the greatly enlarged, bifurcate hemipenes of adult males.

Anolis granuliceps, a small beta anole of uncertain relationship from western Colombia and northwestern Ecuador, shows a similar reduction in the size of the supraocular scales, but the central scales in the supraocular area are slightly enlarged and keeled, while those of *lynchi* are subequal and usually granular. The hemipenes of *granuliceps* are small and not bifurcate, and the small male dewlap is golden orange.

Natural History. All of the Ecuadorian specimens of *A. lynchi* for which there are field notes were collected at night as they slept on low vegetation adjacent to small streams in closed-canopy rain forest. They were sleeping head-up on leaves and small ferns alongside, or overhanging, the creek beds, usually within 1 m of the ground. The Colombian specimens were collected in a forested ravine on low vegetation near a stream during the day. It appears that *A. lynchi* is associated with streamside lowland rain forest habitats, although admittedly collectors may have concentrated on streamside habitats, or the lizards may simply have been easier to see in these areas. Charles W. Myers, who collected the Colombian sample, believes that it is not an aquatic anole in the same sense as *A. poecilopus.* At his collecting site this niche was apparently occupied by *A. macrolepis,* another member of the *lionotus* group. However, the association between *A. lynchi* and streamside forest

habitats seems real, at least in the southern part of its distribution. Despite extensive collecting in the vicinity of Santo Domingo de los Colorados, the only available specimens were found in the immediate vicinity of forest streams. Other anoles found within 200 m of one such creek (2 km E, 1 km N Santo Domingo de los Colorados) include *A. chloris, fraseri, gracilipes, peraccae, princeps,* and an undescribed species related to *vittigerus.*

Discussion. Williams (1976) recognized two South American anoles, *A. poecilopus* Cope and *A. macrolepis* Boulenger, in his *lionotus* species group. He has subsequently described a third, *A. rivalis* Williams, 1984. The group was characterized in Williams' 1976 key by the presence of a zone of enlarged flat or slightly keeled middorsal scales. In *A. macrolepis* and *A. rivalis* the enlarged middorsals are considerably larger than the lateral scales and are arranged in from 11 to 17 longitudinal series. In *A. poecilopus* the enlarged middorsals are only slightly larger than the laterals, into which they grade. In *A. lynchi* the zone of enlarged middorsals is scarcely evident. There are only two slightly larger and flatter paravertebral scale rows, and the difference in size and shape is slight. The lack of an obvious zone of enlarged middorsal scales, and the extreme reduction in the size of scales on the supraocular discs, at first obscured the relationships of *A. lynchi* and suggested an association with the *aequatorialis* group (*sensu* Williams, 1976). However, the presence of transverse processes on the posterior caudal vertebrae made this impossible.

The large bilobed hemipenes of *A. lynchi* provide the clearest morphological evidence linking *A. lynchi* with the *lionotus* species group. Many anoles show a tendency for the distal end of the hemipenis to be bilobed, but few show a strongly forked hemipenis with the bifurcation extending as much as a third the length of the everted organ. This condition characterizes several semiaquatic anoles in Central America and northwestern South America allied to *A. lionotus* Cope. In addition to a semiaquatic streamside habitat and bilobed hemipenes, these lizards share a similar body pattern with distinct lateral stripes. The group consists of six currently recognized species: *A. lionotus* of central Panama, *A. oxylophus* of Costa Rica, Nicaragua and western Panama, *A. poecilopus* of eastern Panama and northwestern Colombia, *A. rivalis* and *A. macrolepis* of western Colombia, and *A. lynchi.* Each is distinct in

external morphology, and occupies largely exclusive ranges. *Anolis lynchi* and *A. macrolepis* have both been collected at Quebrada Guangui in Cauca, Colombia and *A. poecilopus* and *A. lionotus* occur in sympatry in central Panama (Campbell, 1973), but the zones of overlap are probably narrow.

Anolis lynchi is the southernmost representative of the *lionotus* group. The distribution of the South American species of the group is shown in Figure 3. The range of *A. poecilopus*, which on the basis of external similarity seems to be the closest relative of *A. lynchi*, is separated from that of *A. lynchi* by a substantial gap of approximately 1,000 km. The intervening area is inhabitated by *A. macrolepis* and *A. rivalis*, which are not morphologically close to either species.

ACKNOWLEDGMENTS

John D. Lynch collected most of the specimens of the new species and provided information about the localities, field notes, and Kodachrome transparencies. Charles W. Myers of the American Museum of Natural History (AMNH) loaned Colombian specimens and field notes. Ernest E. Williams shared his wealth of knowledge on South American *Anolis* and commented on the manuscript. Stephen Ayala commented on the manuscript and answered questions regarding Colombian specimens. Other specimens were loaned by William E. Duellman, Museum of Natural History of the University of Kansas (KU), W. Ronald Heyer and Ronald I. Crombie, National Museum of Natural History (USNM), and Arnold G. Kluge, University of Michigan Museum of Zoology (UMMZ). My own unsuccessful efforts to collect *Anolis lynchi* in Ecuador were partially funded by Earthwatch and the Center for Field Research of Belmont, Massachusetts and by the Museu de Zoologia of the Universidade de São Paulo. I thank Jeannie Sellmer and Laszlo Meszoly for the illustrations.

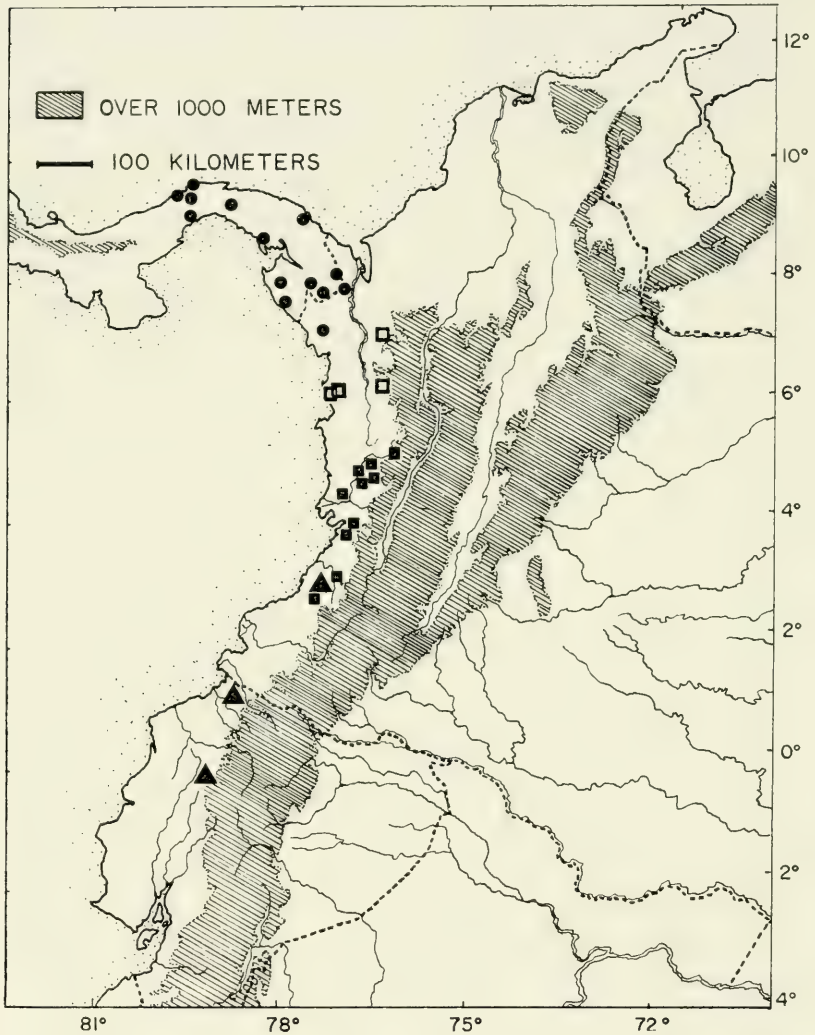


Figure 5. Distribution of the *Anolis lionotus* species group in South America and lower Central America. Triangles: *A. lynchi*, n. sp. Solid squares: *A. macrolepis*. Open squares: *A. rivalis*. Circles: *A. poecilopus*. Localities for *A. macrolepis* and *A. rivalis* were provided by Stephen Ayala and Ernest E. Williams.

LITERATURE CITED

CAMPBELL, H. W. 1973. Ecological observations on *Anolis lionotus* and *Anolis poecilopus* (Reptilia, Sauria) in Panama. Amer. Mus. Nat. Hist. Novitates, **2516**: 1–29.

ETHERIDGE, R. E. 1960. The relationships of the anoles (Reptilia: Sauria: Iguanidae). An interpretation based on skeletal morphology. Ann Arbor, University Microfilms, xiv + 236 pp.

WILLIAMS, E. E. 1976. South American anoles: the species groups. Pap. Avuls. Zool., S. Paulo, **29**: 259–268.

_____. 1984. New or problematic *Anolis* from Colombia. III. Two new semiaquatic anoles from Antioquia and Chocó, Colombia. Breviora Mus. Comp. Zool., No. 478, pp. 1–22.

MUS. COMP. ZOOL
LIBRARY
JUN 17 1985
HARVARD UNIVERSITY

BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 21 JUNE 1985 NUMBER 482

NEW OR PROBLEMATIC *ANOLIS* FROM COLOMBIA. IV. *ANOLIS ANTIOQUIAE*, NEW SPECIES OF THE *ANOLIS EULAEMUS* SUBGROUP FROM WESTERN COLOMBIA.

ERNEST E. WILLIAMS[1]

ABSTRACT. A new species of the *Anolis eulaemus* subgroup of the *A. aequatorialis* species group from the western part of the Departmento Antioquia, Colombia is closer to *A. fitchi* Williams and Duellman of southern Colombia and northern Ecuador than to neighboring *A. ventrimaculatus* Boulenger and *A. eulaemus* Boulenger of the Departments of Valle and Risavalda.

Three adult female *Anolis* from the Cordillera Occidental of Antioquia, Colombia represent a distinctive new species of the *eulaemus* subgroup of the *Anolis aequatorialis* species group. Other members of this subgroup include *A. eulaemus* Boulenger, *A. ventrimaculatus* Boulenger, *A. gemmosus* O'Shaughnessy, *A. maculigula* Williams and *A. fitchi* Williams and Duellman, all ranging farther to the south in Colombia and Ecuador. Several novelties in the genus *Anolis* have recently been discovered in Antioquia, so it seems appropriate to emphasize the interest of the new material by naming this lizard:

[1]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

Figure 1. *Anolis antioquiae*, new species. Female paratype, LACM 72763.

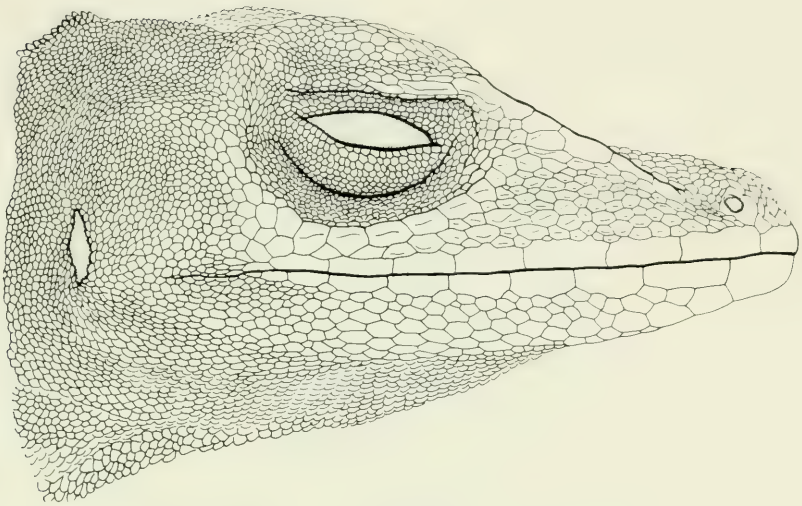


Figure 2. *Anolis antioquiae*, LACM 72763. Lateral view of head.

Anolis antioquiae, new species
(Figs. 1–4)

Type: INDERENA 0277, adult female.

Type locality: Along a road paralleling Quebrada Chaparral, Río San Juan drainage, 10 km E of Andes (town), western Antioquia, Colombia, 2200–2300 m. Philip A. Silverstone, Carlos Arturo Escobar and Luis Carlos Acevedo Cuartas coll., July 1971.

Paratypes. Antioquia: LACM 72763, adult female, same locality as type. CSJ 310, adult female, Urrao.

Description. Head. Head scales minute, anteriorly weakly uni- to multicarinate, posteriorly pustulose. Sixteen to 19 scales across snout between second canthals. Six to seven scales border rostral posteriorly. Anterior nasal scale separated from rostral by one scale or in contact.

Supraorbital semicircles separated medially by four to five scales. The medial supraocular scales enlarged, wrinkled or keeled, but supraocular disk not or very weakly defined. Three short superciliaries on each side, followed by granules. *Canthus projecting laterally, sharp-edged, slightly overhanging loreal region.* Second and third or third and fourth or fourth and fifth scales longest. Ten to twelve loreal rows.

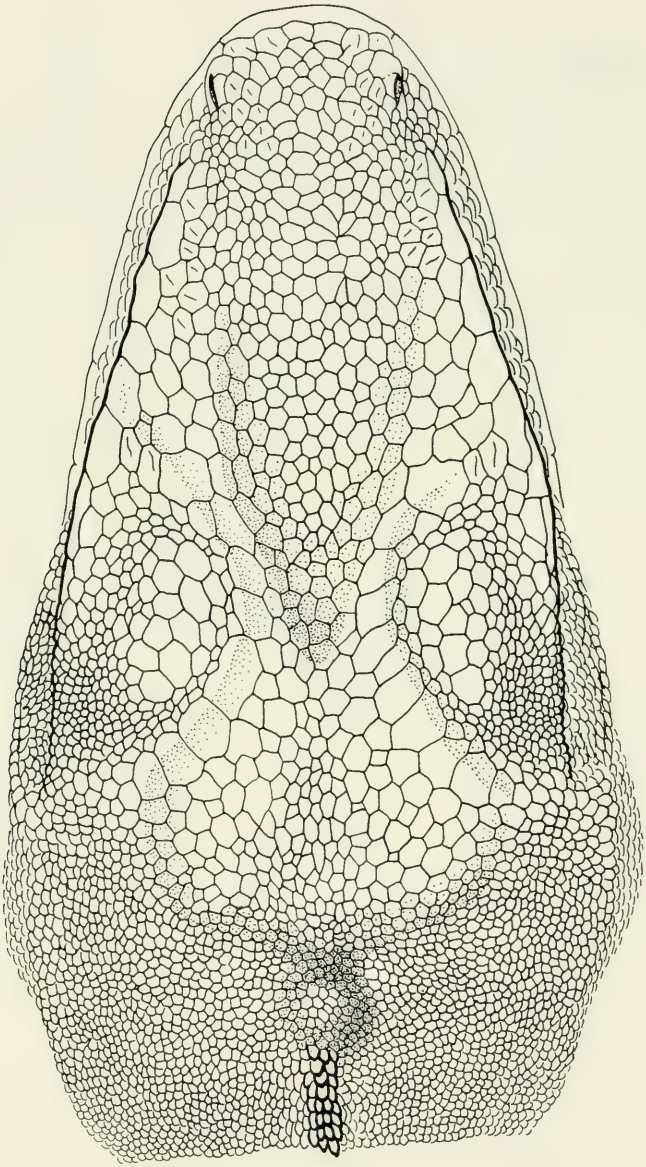


Figure 3. *Anolis antioquiae*, LACM 72763. Dorsal view of head.

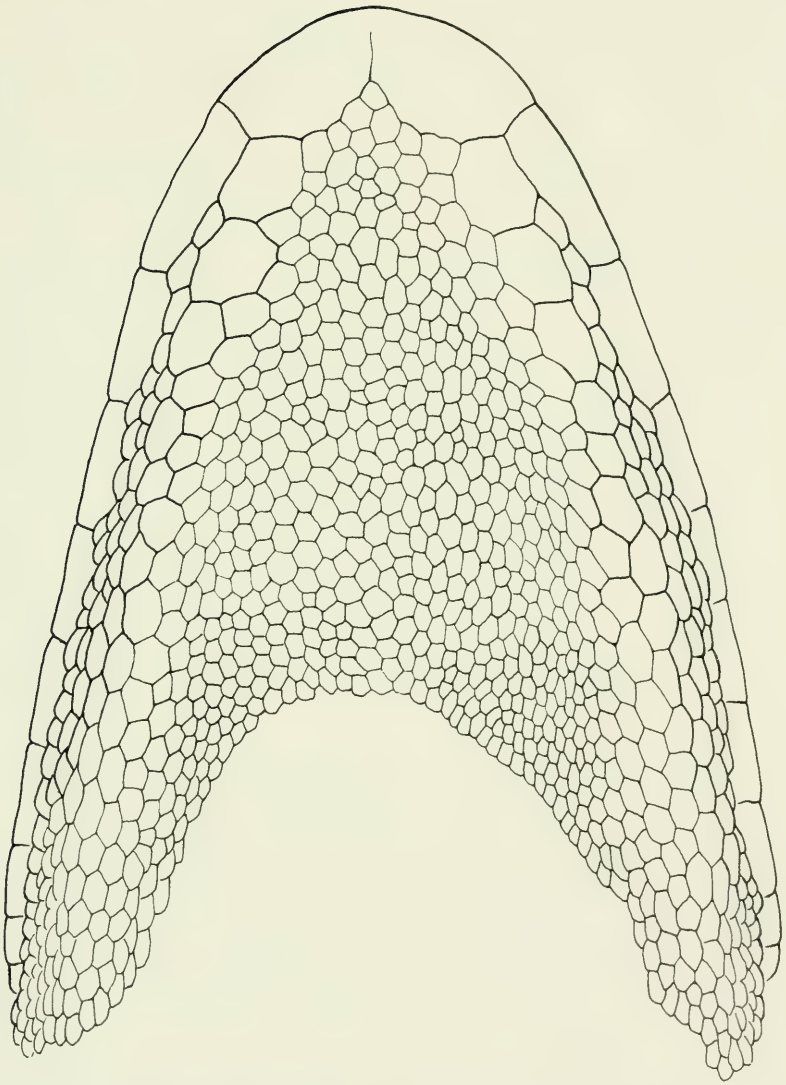


Figure 4. *Anolis antioquiae*, LACM 72763. Ventral view of head.

Temporals and supratemporals granular. An intertemporal double row of enlarged scales hardly indicated. *No interparietal.* Scales in the interparietal area granular posteriorly, grading into parietal area, bounded by oblique lateral ridges which converge on but do not meet a blunt occipital knob, larger scales alongside the supraorbital semicircles. Ear moderate but less than half eye aperture.

Suboculars weakly keeled, narrowly and irregularly in contact with the supralabials. Six to seven supralabials to below the center of the eye.

Mental completely or incompletely divided, each half as wide as deep, indented medially by six to seven small swollen smooth scales between the large smooth sublabials, only the first of which on each side is in contact with the infralabials (on one side of INDERENA 0277 the second sublabial also is in contact with the infralabials). Central gular scales smooth or keeled, imbricate, projecting, subequal, becoming rather abruptly larger, laterally adjacent to the infralabials.

Trunk. A central zone of small keeled juxtaposed scales grading into smaller projecting and bluntly or sharply pointed flank scales that are juxtaposed or separated by minute granules. Ventrals larger, smooth, juxtaposed or subimbricate, not in transverse rows.

Dewlap. Moderate (female), extending posteriorly to the level of the axilla. Scales close packed, more or less projecting, smaller than ventrals.

Limbs and digits. Scales on limbs uni- to multicarinate, the largest (on anterior thigh) as large or larger than ventrals, on digits multicarinate. Digital dilations narrow, 21 to 22 lamellae under phalanges ii and iii of fourth toe.

Tail. Compressed, no dorsal crest. Tail scales small, larger below, all keeled except those under the base of tail smooth. Two middorsal rows enlarged.

Size. The snout-vent length of the INDERENA type is 72 mm, of CSJ 310 77 mm, and of LACM 72763 74 mm. The tail is broken in all three specimens.

Color (as preserved). Light purplish with brown markings expanding at intervals on the dorsum (Type and LACM 72763) or dark purplish with a dorsal zone brown with a black line on each side (CSJ 310). Throat and belly very weakly spotted on a light grey

Table 1. Comparison of *Anolis antioquiae* and *A. fitchi*.

	antioquiae	fitchi
head scales	minute, uni- and multi-carinate	small, multicarinate, tuberculate or wrinkled
number between second canthals	16–19	11–18
postrostrals	6–7	6–9
superciliaries	the *3 anterior short* followed by granules	one anterior elongate followed by one or two shorter ones and granules
canthals	*sharply keeled, slightly overhanging loreals*	blunt, *not* overhanging loreals
loreal rows	10–12	8–11
interparietal	none	smaller than ear, separated from semicircles by 3–6 scales
suboculars	narrowly and irregularly in contact with supralabials	separated from supralabials by one row or narrowly in contact
supralabials to center of eye	6–7	8–11
mental	*indented* medially by 6–7 small scales between *large sublabials*	*in transverse contact* with 5–8 scales between infralabials. *Sublabials not* differentiated.
middorsals and flank scales	a dorsal *zone* of keeled juxtaposed scales grading into smaller conical flank scales juxtaposed or separated by minute granules	2–4 middorsal rows slightly enlarged, keeled, swollen, subimbricate, lateral granules conical, juxtaposed
ventrals	larger than dorsals, smooth, subimbricate or juxtaposed, *not* in transverse rows	larger than dorsals, smooth, imbricate or subimbricate, tending to be in transverse rows
lamellae under 4th toe	21–22	21–24

ground (Type) or light purplish laterally smudged medially (CSJ 310). The limbs are very weakly banded, the tail darkish above, lighter below. Dewlap white, blotched and spotted with intense black.

Color in life. P. A. Silverstone has provided color notes for the Type and LACM 72763: "Dorsum green with black median stripe with paired light green spots. Venter brown with white spots. Dewlap red orange with black blotches and yellow border."

Ecology. Silverstone reports the two specimens collected by his party "on ferns at the edge of forest next to pasture."

Comparisons. *Anolis antioquiae* is closest to recently described *Anolis fitchi* Williams and Duellman. In both the female has a blotched dewlap. In both there is a noticeable indication of a small round parietal spine or convexity (Fig. 2) just anterior to the enlarged median name scales. This small prominence is not evident in other species of the group. Of the other recognized species of the *eulaemus* subgroup, two—*A. ventrimaculatus* and *A. gemmosus*—entirely lack a dewlap in females. In the one female referred to *A. eulaemus* the dewlap is much reduced, apparently with uniformly dark skin. All three examined specimens of *A. antioquiae* lack an interparietal; this scale is always present in *A. fitchi* and in *A. eulaemus*, but sometimes absent in *A. gemmosus* and often so in *A. ventrimaculatus*.

A. antioquiae is unique in one respect: the very sharp canthal ridge projecting above the loreal region, although an apparently trivial character, has not been seen by me in any other species of the group or indeed in any *Anolis*. Within the group the three subequal short superciliaries are unusual. The median angular indentation of the mental by postmental scales contrasts with the straight transverse border seen at the mental gular contact in *A. fitchi*. The conical flank scales often surrounded by granules are again very different from other members of the group.

Although this species is apparently allopatric to—somewhat to the north of—*A. eulaemus* and *A. ventrimaculatus*, and although only females are known (and the female reported as that of *eulaemus* is questionably so referred), there is no question of conspecificity or even of very close relationship. Even with *A. fitchi*, very distant in Napo in Ecuador and Putamayo in Colombia, despite more resemblances, there is no demonstration of close affinity except for position with the same subgroup of a species group.

ACKNOWLEDGMENTS

I am grateful to Jorge Hernandez of INDERENA, John Wright and Robert Bezy of the Los Angeles County Museum (LACM), and Marco A. Serna of the Colegio San Jose, Medellin, Colombia (CSJ) for the loan of specimens. Laszlo Meszoly made the drawings.

LITERATURE CITED

WILLIAMS, E. E., AND W. E. DUELLMAN. 1984. *Anolis fitchi*, a new species of the *Anolis aequatorialis* group from Ecuador and Colombia, pp. 257–266. *In* Seigel R. A. *et al.* (eds.), Vertebrate Ecology and Systematics—A Tribute to Henry Fitch, Lawrence, Kansas.

MUS. COMP. ZOOL.
LIBRARY
JUN 17 1985
HARVARD
UNIVERSITY

BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 21 JUNE 1985 NUMBER 483

NOTES ON *PRISTIDACTYLUS* (SQUAMATA: IGUANIDAE)

RICHARD ETHERIDGE[1] AND ERNEST E. WILLIAMS[2]

ABSTRACT. *Pristidactylus* is diagnosed as a genus of austral South American anoloid iguanid lizards allied to *Enyalius* and possibly paraphyletic with respect to *Leiosaurus, Aperopristis*, and *Diplolaemus*. West of the Andes *Pristidactylus torquatus* occurs in forested coastal areas and the inland cordilleras of central Chile; *P. valeriae* (new comb.) and *P. alvaroi* (new comb.) are restricted to disjunct patches of relict forests to the north in Santiago Province. East of the Andes four species occur in Argentina. *P. casuhatiensis* lives in high, wet, rocky meadows atop the Sierra de la Ventana in southern Buenos Aires Province, and *P. achalensis* occurs in a similar habitat atop the Sierra de Córdoba in Córdoba Province. *P. scapulatus* is known from arid, rocky habitats at disjunct localities in the cordilleras and precordilleras from western Catamarca Province southward to Mendoza Province, and on isolated basaltic mesetas at lower altitudes from Mendoza southward to Chubut Province. In cordilleran and precordilleran populations adult females virtually lose the bold juvenile pattern whereas those from the basaltics do not. Although the latter are not recognized nomenclatorially, the name *P. araucanus* is available for them. *P. fasciatus*, type species of the genus, lives in a narrow belt of sandy steppe from San Juan Province southward to Río Negro and extreme southern Buenos Aires Provinces. It has frequently been incorrectly referred to as *P. araucanus*. *Leiosaurus bardensis* is a synonym of *P. fasciatus*. A key to the species of *Pristidactylus* is provided.

INTRODUCTION

Pristidactylus is a genus of austral South American iguanid lizards with a disjunct distribution in Chile and Argentina, and an exceedingly complex taxonomic history. Fitzinger (1843: 58) described *Pristidactylus* as a subgenus of *Leiosaurus* Duméril and Bibron, 1837, and designated *Leiosaurus fasciatus* Duméril and

[1]Department of Biology, San Diego State University, San Diego, California 92182.
[2]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

Bibron, 1837 as its type species. Boulenger (1885: 127) employed *Pristidactylus*, but only for the species *fasciatus*. In this century, up until 1976, *fasciatus* and all of the other species now referred to *Pristidactylus* were variously placed in *Leiosaurus, Urostrophus* Duméril and Bibron, 1837 and *Cupriguanus* Gallardo, 1964. In 1976 Etheridge (*in* Paull, Williams, and Hall, 1976: 10) pointed out that if Barrio (1969) was correct in placing *Cupriguanus araucanus* Gallardo, 1964 in the synonomy of *Leiosaurus fasciatus* Duméril and Bibron, 1837 and if the latter were congeneric with *Cupriguanus achalensis* Gallardo, 1964, type species of *Cupriguanus*, then *Cupriguanus* is a junior synonym of *Pristidactylus* Fitzinger, 1843. In this work seven species are referred to *Pristidactylus*: *achalensis* Gallardo, 1964; *alvaroi* Donoso-Barros, 1975; *casuhatiensis* Gallardo, 1968; *fasciatus* Duméril and Bibron, 1837; *scapulatus* Burmeister, 1861; *torquatus* Philippi, 1861; and *valeriae* Donoso-Barros, 1966.

Pristidactylus in this modern sense has never had a proper diagnosis, nor have the species within it been adequately distinguished from one another. We plan a future, more formal review of *Pristidactylus* and related taxa; we here propose only to provide a diagnosis and discussion of the genus as now understood, enough description of the named forms to permit their recognition, and lastly a key which is arranged to display the relationships of the species as we now understand them. These notes are based on examinations of 221 specimens of *Pristidactylus* in European, North and South American museums (see Acknowledgments), and field work in Argentina by Etheridge in late January, February, and March during the austral summer of 1983.

Pristidactylus Fitzinger 1843

1843 *Leiosaurus (Pristidactylus)* Fitzinger, Syst. Rept., Wien, **1:** 16.—Type species (by indication): *Leiosaurus fasciatus* Duméril and Bibron 1837.

1845 *Leiosaurus (Pentadactylus)* Gray, Cat. Spec. Liz. Brit. Mus., London, 224.—Type species (by monotypy and original designation) *Leiosaurus fasciatus* D'Orbigny in Dumeril and Bibron 1837.

1885 *Pristidactylus*—Boulenger, Cat. Liz. Brit. Mus., London, **2:** 127.

1964 *Cupriguanus* Gallardo, Neotropica, B. Aires, **10**(33): 127.—Type species (subsequent designation by Gallardo, 1967: *Cupriguanus achalensis* Gallardo 1964.)

1976 *Pristidactylus*—Etheridge *in* Paull, Williams, and Hall, Breviora, Mus. Comp. Zool., No. 441, p. 10.

Diagnosis. Pristidactylus is a member of the "anoloid" group of iguanid genera, specified by the acquisition of endolymphatic sacs that extend back between the parietal and occipital bones into the dorsal neck musculature (Etheridge and de Queiroz, in preparation). Within anoloids *Polychrus* is considered the sister group of the remaining genera, the latter having lost femoral pores and acquired a spinulate Oberhäuchen with flat cell borders. Within this latter group *Pristidactylus* together with *Diplolaemus, Leiosaurus, Aperopristis* and *Enyalius* retain four pairs of sternal ribs and have acquired a unique structure of the distal two or three subdigital scales: each has a median longitudinal groove. Although grooved distal subdigitals are obscure or lacking in forms with distinctly multicarinate subdigital scales (*P. fasciatus, A. catamarcensis, A. paronae, E. leechii*, and *E. brasiliensis*), their presence is considered a derived characteristic of the group, their absence the result of loss. This subgroup containing *Pristidactylus* forms the sister taxon to a group formed by the remaining anoloid genera: *Urostrophus, Anisolepis, Aptycholaemus, Chamaeleolis, Phenacosaurus, Chamaelinorops*, and *Anolis*, all of which have three rather than four pairs of sternal ribs.

Relationships among the genera that form the subgroup containing *Pristidactylus* remain unresolved, and a preliminary analysis indicates that *Pristidactylus* itself may be paraphyletic. Nevertheless, *Pristidactylus* can be diagnosed within this group. It differs from *Aperopristis, Diplolaemus*, and *Leiosaurus* in having a black bar within the antehumeral fold and marked sexual dichromatism; it further differs from *Aperopristis* and *Leiosaurus* in having fully autotomic caudal vertebrae and a different color pattern, and from *Diplolaemus* in possessing pterygoid teeth. *Pristidactylus* differs from *Enyalius* in having the caudal scales smooth proximally and keeled distally (keeled throughout in *Enyalius*); slightly convex rather than conical mesoptychials; wide, smooth, scarcely imbricate, lamellarlike supradigitals rather than sharply unicarinate, rhomboidal and imbricate supradigitals; the prefrontal-frontonasal part of the skull roof rounded rather than flat; a more robust body (somewhat compressed in *Enyalius*); shorter limbs (adpressed hind limb reaches to between the antehumeral fold and orbit in *Pristidactylus*,

to the orbit or beyond in *Enyalius*); and a shorter tail (tail/snout-vent 0.73–1.60 in *Pristidactylus*, 1.60–3.30 in *Enyalius*).

Juveniles of *Pristidactylus* and *Diplolaemus* have a light grey or yellowish background with bold, dark crossbands over the head, body, tail, and limbs, with a characteristic horseshoe-shaped marking over the back of the head, and the crossbands of the back usually constricted laterally. In both sexes with increasing size the dark markings typically break up or acquire irregular borders. Large adult male *Pristidactylus* become nearly unicolor except for a conspicuous, black antehumeral bar, and have at most only a faint trace of the juvenile pattern. The juvenile pattern, though altered, remains bold in adult females, except for the northern populations of *P. scapulatus*. The juvenile markings show various patterns of ontogenetic change in *Diplolaemus*, but never disappear entirely, and are identical in large individuals of both sexes. The distinctive butterfly or fleur-de-lis markings of *Leiosaurus* and *Aperopristis* are present at hatching and change little in either sex. Thus, marked sexual dichromatism is a characteristic of *Pristidactylus*, shared with *Enyalius*, but distinguishing it from *Aperopristis, Diplolaemus* and *Leiosaurus*.

Boulenger in 1885 transferred *Leiosaurus torquatus*, and in 1889 *Leiosaurus scapulatus*, to *Urostrophus* Duméril and Bibron, 1837; type species *U. vautieri* Duméril and Bibron, 1837. Gallardo (1964) recognized that a number of differences exist between *Urostrophus vautieri* and *Leiosaurus scapulatus*. He proposed the genus *Cupriguanus* to include *scapulatus* and two additional species from Argentina described in the same work, *araucanus* from Laguna Blanca, Neuquén Province, and *achalensis* from the Pampa de Achala in Córdoba Province. He further suggested that *Leiosaurus torquatus* probably should be transferred to *Cupriguanus*. Gallardo pointed out that *Cupriguanus* differs from *Leiosaurus* (in which he included *Diplolaemus* and *Aperopristis*) in having compressed and pectinate infradigitals at the bases of the first, second, and third toes of the hind foot. The pectinate scales on the inner border of the first, second, and third toes, conspicuous in *P. fasciatus* and emphasized by Gallardo (1964) as characteristic of *Cupriguanus*, are not uniformly developed in all species of *Pristidactylus*, and are least prominent in *P. casuhatiensis*. Also, these scales are conspicuously swollen, though not pectinate, in *Diplolaemus*, so that this feature is

not as clear-cut as Gallardo thought. Gallardo also pointed out that *Pristidactylus* differs from *Urostrophus* in having a shorter tail, more labial scales and more scales between the supralabials and suboculars, no projecting scales around the eye, the trunk and tail not compressed, and the fourth toe shorter. Gallardo's (1979) use of the binomial *Pristidactylus vautieri* for *Urostrophus vautieri* was unjustified and probably unintended. As indicated earlier, *Urostrophus* is a member of the sister taxon of the group containing *Pristidactylus*, distinguished from the latter by the loss of a pair of sternal ribs and the absence of grooved distal subdigital scales. Thus, although not all of Gallardo's characters for *Cupriguanus* (= *Pristidactylus*) are useful, *Pristidactylus* can be distinguished from *Urostrophus* as well as from other anoloid genera as indicated in the diagnosis.

Cei (1973a) compared *Cupriguanus* with *Leiosaurus, Aperopristis*, and *Diplolaemus*. His concept of *Cupriguanus* was based upon the Argentinian species, *achalensis, scapulatus, casuhatiensis,* and *"fasciatus" (=araucanus). Leiosaurus bardensis (=Pristidactylus fasciatus)* was included with *belli* and *catamarcensis* in the genus *Leiosaurus*, and *Aperopristis* was considered monotypic with the species *paronae. Diplolaemus* included the species *darwinii, bibronii,* and *leopardinus*. He pointed out correctly that *Diplolaemus* differs from the others in lacking pterygoid teeth. The subocular was said to be elongate in *Diplolaemus* and *Cupriguanus*, represented by an arc of small, subequal scales in *Leiosaurus* and *Aperopristis*; however, we find this condition variable in both *Diplolaemus* and *Pristidactylus*. The subdigital scales were said to be smooth in *Diplolaemus* and *Cupriguanus*, unicarinate or multicarinate in *Leiosaurus*, and multicarinate in *Aperopristis*. The subdigital scales are smooth in *Diplolaemus* and multicarinate in *Aperopristis*; however, in *Pristidactylus* they are smooth, indistinctly unicarinate or multicarinate. Cei's description of the subdigital scales of *A. paronae* and *L. catamarcensis* as having three to five distinct keels is correct, but his statement that the subdigital scales of *belli* have one to three keels is not entirely in accord with our observations. In 64 specimens of *L. belli* from Chubut, Mendoza, Neuquén, Río Negro, and Santa Cruz Provinces we find the subdigital scales either entirely smooth, as stated in the type description (Duméril and Bibron, 1837), or with one, rarely two, indistinct keels, as mentioned

by Koslowsky (1898). The distal caudal scales were said to be smooth in *Diplolaemus*, but we find they are keeled in *D. darwinii*, as first noticed by Stejneger (1909).

A precis of the recognized species of *Pristidactylus* follows:

Pristidactylus fasciatus (Duméril and Bibron 1837)

1837 *Leiosaurus fasciatus* Duméril and Bibron, Erpét. Gén., Paris, **4:** 244.—Type locality: not specified, specimen shipped from Buenos Aires. Restricted type locality (D'Orbigny, 1847): Carmen de Patagones, Buenos Aires Province, Argentina.

1843 *Leiosaurus (Pristidactylus) fasciatus*—Fitzinger, Syst. Rept., Wien, **1:** 58.

1845 *Leiosaurus (Ptenodactylus) fasciatus*—Gray, Cat. Spec. Liz. Coll. Brit. Mus., London, 224.

1885 *Pristidactylus fasciatus*—Boulenger, Cat. Liz. Brit. Mus., London, **2:** 127.

1896 *Pristidactylus fasciatus*—Koslowsky, Revta Mus. La Plata, **7:** 447.

1933 *Leiosaurus fasciatus*—Burt and Burt, Trans. Acad. Sci. St. Louis, **27**(1): 30.

1968 *Leiosaurus bardensis* Gallardo, Neotropica, Buenos Aires, **14**(43): 5, unnumb. Fig.—Type locality: Puelen, Cochicó, Altos de Chochicó, La Pampa Province, Argentina.

1973 *Cupriguanus bardensis*—Cei and Roig, Deserta, Mendoza, **4:** 71.

1978a *Pristidactylus bardensis*—Cei and Castro, Publ. Occ. Inst. Biol. Anim. Univ. Nac. Cuyo, Ser. Sci., **5:** 3.

Diagnosis. Pristidactylus fasciatus is unique within the genus in having multicarinate subdigital scales and the tail less than 50% of the total length.

Taxonomy. The type description of *fasciatus* was based upon a juvenile specimen (42 mm snout-vent) collected on the wall of the fort at Carmen de Patagones in extreme southern Buenos Aires Province, just north of the mouth of the Río Negro. Duméril and Bibron (1837: 244) attribute the name to D'Orbigny, who collected the animal and for a time observed it alive. D'Orbigny (1847), in an expanded description with notes on the live animal, described it as a "charming species with all of the body a lively yellow, the top of the head brown, two large, transverse bands on the back of the head, six on the back all interrupted on the flanks. The upper part of the tail is likewise ringed with black, just as are the limbs."

Duméril and Bibron's (1837) description of *fasciatus* is for the most part applicable to juvenile individuals of all species now referred to *Pristidactylus*, except that the subdigital scales are said to be multicarinate, and the internal border of the foot has a denticulation, both variable in the genus, and the tail is shorter than in

other forms. That the tail was mutilated was noted in the type description, but the figure provided by D'Orbigny (1847) shows an animal with a complete tail, and when measured on the illustration the tail appears to be between 0.8 and 0.9 times the snout-vent length.

Boulenger (1885) listed *Pristidactylus fasciatus* on the authority of Duméril and Bibron (1837), but inexplicably stated that the tail is nearly twice as long as the head and body. Koslowsky (1896) reported specimens under that name from Río Negro and Neuquén, the latter having subdigital keels completely lacking, and later Koslowsky (1898), under the name *Leiosaurus fasciatus*, reported a juvenile from Neuquén with subdigital scales tricarinate at the extremities but otherwise smooth. In the latter the tail/snout-vent ratio was 1.18. It seems likely that Koslowsky's specimens from Neuquén are referable to the form described from Laguna Blanca by Gallardo (1964) as *Cupriguanus araucanus* rather than to *P. fasciatus*. In the former, the tail is longer than the snout-vent length and the subdigital scales are smooth except for the grooved distal subdigitals. Koslowsky's Río Negro specimen was not described. Koslowsky's (1898) use of the binomial *Leiosaurus fasciatus* was followed by Burt and Burt (1933) and Lieberman (1939).

Barrio (1969) compared the types of *Pristidactylus fasciatus* and *Cupriguanus araucanus* Gallardo, 1964. He concluded that they were synonyms because in both the juvenile pattern was one of distinctive dark crossbands on the head, body, limbs, and tail; there were pectinate scales on the infradigitals of toes 1, 2, and 3; and measurements taken from D'Orbigny's (1847) figure yield a snout-vent/tail ratio of 0.89, only slightly larger than that of *C. araucanus*. However, the distinctive juvenile markings are characteristic and very similar in all species of *Pristidactylus* and *Diplolaemus*, most other species of *Pristidactylus* have pectinate subdigitals on the foot, and according to Gallardo's (1964) figures and our own calculations the snout-vent/tail length ratio in specimens from Laguna Blanca, the type locality of *araucanus*, is greater than 1.0. Barrio noted that Gallardo had specifically rejected the synonomy of *araucanus* with *fasciatus* because of the shorter tail in the latter, and that Gallardo must have obtained his measurements from the illustration of D'Orbigny, Although Barrio directly compared the holotypes of both species he apparently failed to note the presence of distinctly multicarinate subdigitals in *fasciatus*, as contrasted with the smooth

subdigitals of *araucanus*. The synonomy of *araucanus* with *fasciatus* was accepted by Cei (1973a, 1973b, 1975, 1979), Cei and Castro (1978a, 1978b), and Cei and Roig (1973).

Gallardo (1968) described *Leiosaurus bardensis* from Cochicó, La Pampa Province and reported additional specimens from Ishigualasto, San Juan Province, some distance north of the type localities of *fasciatus* and *araucanus*. He compared the species in detail with *Diplolaemus darwinii* and *D. bibronii*, but not with any of the species now referred to *Pristidactylus*. The species was recognized as *Cupriguanus bardensis* by Cei and Roig (1973), and as *Pristidactylus bardensis* by Cei and Castro (1978a, 1978b). Its distinctive features, i.e., multicarinate subdigital scales, pectinate subdigitals on the foot, and a tail shorter than head and body, are just those characteristics which distinguish *P. fasciatus* from other species of *Pristidactylus*. We have examined the types of *bardensis* and *fasciatus* and a dozen other specimens from Río Negro, Mendoza, and San Juan Provinces, and we find they agree in all essential details.

Distribution and Habitat. Pristidactylus fasciatus has been taken at widely scattered localities between Ishigualasto (±30° 10′S, 57° 50′W) at about 1,700 m altitude in the north and the type locality near sea level in the south. All records are within the Southern Chaco Province, or Monte (Cei, 1979). Cei and Castro (1978a) stated that in the Bermejo Basin of San Juan Province it occurs in areas of sand dunes. In Mendoza Province the species lives on flat, sandy steppe, at altitudes between 1,000 and 1,750 m, and Gallardo (1968) stated that at Chochicó in La Pampa Province (type locality of *bardensis*) it lives in loose sand, in small burrows of *Microcavia sp.* constructed in mounds of sand that accumulate around the bases of *Prosopis alpataco*. Other species of Argentinian *Pristidactylus* appear always to be associated with rocky areas, and at the same latitudes occur at higher altitudes. South of La Pampa Province there are no specific locality records except for the type locality, but Koslowsky (1898) reported the species from Río Negro Province, and we have seen a specimen in the Zoologiske Museum, Universitetes Københaven also from "Rio Negro."

Pristidactylus scapulatus (Burmeister)

1861 *Leiosaurus scapulatus* Burmeister, Reise La Plata-Staat., Halle, **2:** 523. Type locality: Sierra de Uspallata, near Uspallata, about 5,000 ft. altitude, Mendoza Province, Argentina.

1861 *Leiosaurus multipunctatus* Burmeister, Reise La Plata-Staat., Halle, **2:** 524. Type locality: Sierra de Uspallata, near Paramillo, about 8,000 ft. altitude, Mendoza Province, Argentina.

1889 *Urostrophus scapulatus*—Boulenger, Proc. Zool. Soc. London, 144; Pl. 15, Fig. 2.

1941 *Leiosaurus scapulatus*—Müller, Zeitschr. f. Naturwiss, **94:** 184.

1964 *Cupriguanus araucanus*—Gallardo, Neotropica, B. Aires, **10**(37): 129; Fig. 2, 3 —Type locality: Laguna Blanca, Neuquén Province, Argentina.

1964 *Cupriguanus scapulatus*—Gallardo, Neotropica, B. Aires, **10**(37): 128.

1976 *Pristidactylus scapulatus*—Etheridge, *in* Paull, Williams, and Hall, Breviora, Mus. Comp. Zool., No. 441, p. 10.

Diagnosis. Pristidactylus scapulatus differs from *P. fasciatus* and *P. casuhatiensis* in having perfectly smooth subdigital scales, from *P. achalensis* in having the crowns of the posterior marginal teeth slightly tapered with small anterior and posterior cusps, and from the Chilean forms (*torquatus, alvaroi*, and *valeriae*) in having one or two scales interposed between the nasal and lateral postrostral scales.

Taxonomy. The descriptions of *Leiosaurus scapulatus* and *L. multipunctatus* Burmeister, 1861 were accompanied by the description of a third species, *Leiosaurus marmoratus*, from several localities west of Catamarca. Boulenger (1889) stated that *scapulatus* represented the adult male, *multipunctatus* the adult female, and *marmoratus* the juveniles of a single species, which he referred to as *Urostrophus scapulatus*. Müller (1928) pointed out that the types of *marmoratus* belonged to the genus *Phrynosaura* Werner *in* Burger, 1907 (subsequently transferred to *Ctenoblepharis* by Cei [1974] and then to *Liolaemus* [Cei, 1980]). Müller (1941) later confirmed Boulenger's synonomy of *multipunctatus* with *scapulatus* after comparing the types at the Museum in Halle.

As presently recognized, *Pristidactylus scapulatus* is a species of the high cordilleras and precordilleras of western Argentina in the provinces of Catamarca, San Juan and Mendoza (Cei, 1979). However, we now believe that specimens from the basaltic tablelands of southern Mendoza, western Neuquén and southern Chubut provinces, previously referred to *P. araucanus* and later to *P. fasciatus* (see above discussion under *fasciatus*), may be conspecific with *P. scapulatus*. In characters of scalation and proportions, and in the color pattern exhibited by adult males, specimens from the cordilleras and precordilleras cannot be distinguished from those from the basaltic tablelands. In these populations as in all other forms of *Pristidactylus*, the bold juvenile pattern becomes progressively more obscured

in males, becoming faint or fading entirely, except for the black antihumeral bars, in large adults.

Adult females from the basaltic tablelands do, however, differ from those of the cordilleras and precordilleras in the extent to which they retain the juvenile pattern. Females 98 mm snout-vent length and larger, from northwestern San Juan Province, and from the Sierra de Uspallata and the vicinity of Paso de Choique in western Mendoza Province usually have numerous scattered dark brown spots on both upper and lower surfaces, but retain only a faint indication of the juvenile crossbands (see Boulenger, 1889, Fig. 2). Those from the basaltic meseta around Volcán Payún in southwestern Mendoza Province, from the vicinity of Laguna Blanca in western Neuquén Province, and from Meseta Canquél in southern Chubut Province, also usually have scattered dark spots, but retain with little fragmentation or loss of contrast the bold pattern of juveniles. Especially prominent is the dark, horseshoe-shaped mark across the back of the head. Retention of a bold pattern in adult females is characteristic of all other species of *Pristidactylus*, thus the loss of pattern in adult females in the cordilleras and precordilleras is unique within the genus.

A question that we have not resolved to our own satisfaction is how to treat this apparent step-clinal variation in the ontogenetic development of the female color pattern taxonomically. Our six populations are widely separated from one another, except for Paso del Choique and Payún, where the step cline is abrupt. The pattern of small, dark spots on a washed-out greyish background characteristic of the Cordilleran females, like that of the males, matches very well the mostly granitic rocks of their habitat, whereas the bold female pattern is more cryptic on the dark brown, eroded substrate of the basaltic mesetas. We may be dealing with relict populations that are now no longer in contact, and the situation appears comparable to a chain of islands extending from north to south, so that any taxonomic decision must perforce be arbitrary.

Serological comparisons of specimens from Uspallata, Choique, Payún, and Batrá (near Payún) show a high degree (>84%) of homogeneity (Cei and Castro, 1975). Future karyological, electrophoretic or immunological studies may shed light on the problem. For now, however, we follow a conservative nomenclature, formally recognizing only *scapulatus*, although in the key below we utilize adult

female color pattern and locality to separate the cordilleran and precordilleran populations from those of the basaltics. If the latter are eventually recognized taxonomically the name *P. araucanus* is available (see discussion under *P. fasciatus*).

Distribution and Habitat. The most northerly record is an unspecified locality in the high cordilleras of Catamarca Province (Koslowsky, 1895). In northwestern San Juan Province at an altitude of 3,800 m in the Reserva Provincial de San Guillermo (29°18′S, 69°15′W) they are closely associated with granitic outcrops and live in burrows under stones or at the bases of small bushes, and appear to be active in the early morning and late afternoon. They occur in similar habitats but at lower altitudes in the Sierra de Uspallata (32°30–41′S, 69°00–06′W; 2,000–3,000 m) and the vicinity of Paso de Choique (36°25–27′S, 69°25–45′W; 1,800–2,000 m) in western Mendoza Province. Fewer than 50 km eastward of Paso de Choique they occur on the basaltic meseta dominated by Volcán Payún (36°26′S, 69°16–25′W; 1,800–2,000 m), where they are also closely associated with stony areas and are active in the morning and late afternoon. Likewise they occur in similar habitats but at lower altitudes to the south, in the vicinity of Laguna Blanca (39°03–45′S, 70°23–37′W; 1,200 m) in western Neuquén Province, and the Meseta Canquél (44°10–33′S, 68°16–20′W; 900 m) in southern Chubut Province. A single specimen is known from Puerto Madryn on the coast in northeastern Chubut.

Pristidactylus achalensis (Gallardo)

1964 *Cupriguanus achalensis* Gallardo, Neotropica, Buenos Aires, **10**(33): 132; Fig. 4.—Type locality: Posta de Pampa de Achala, Córdoba Province, Argentina.

1976 *Pristidactylus achalensis*—Etheridge *in* Paull, Williams, and Hall, Breviora, Mus. Comp. Zool., No. 441, p. 10.

Diagnosis. Pristidactylus achalensis is unique within the genus in having the crowns of the posterior marginal teeth rather strongly compressed linguo-labially, flared in an anterior-posterior direction, and deeply cusped, and in having an adult male color pattern of uniform bright green with an immaculate yellowish belly.

Distribution and Habitat. The species is limited to a small region in western Córdoba Province, from the Pampa de San Luís (31°20′S, 64°46′W) in the north, southward at altitudes of 2,000 to

2,500 m to Cerro Champaqui (31°59′S, 64°56′W). It is abundant on the Pampa de Achala, where the habitat is a high pampa with many low rock outcrops that emerge from a wet meadow covered with low herbaceous vegetation. Numerous small sinkholes full of rain water dot the landscape. The bright green adult males are conspicuous throughout the day. Unlike other members of the genus this species is omnivorous, feeding on a variety of insects, including butterflies, and flowers (di Tada et al., 1977a and 1977b). Its diet is reflected in the species' unique tooth form. Gallardo (1967) reported that 130 individuals were obtained by two collectors in a period of three hours on Cerro Champaqui in February.

Pristidactylus casuhatiensis (Gallardo)

1968 *Cupriguanus casuhatiensis* Gallardo, Neotropica, B. Aires, **14**(43): 2; unnumb. fig. —Type locality: Sierra de la Ventana, Buenos Aires Province, Argentina.

1976 *Pristidactylus casuhatiensis*—Etheridge *in* Paull, Williams, and Hall, Breviora, Mus. Comp. Zool., Cambridge, No. 441, P. 10.

Diagnosis. Pristidactylus casuhatiensis is unique within the genus in having one or two indistinct keels on most of the subdigital scales, the posterior marginal tooth crowns swollen, and in having an adult male color pattern consisting of a green background with a fine, dark reticulum, especially prominent on the sides; their venter is immaculate yellow. The adult females have a brown background color with obscure transverse bars.

Distribution and Habitat. The species is known only from Cerro Tres Picos (38°27′S, 62°12′W) and Cerro de la Ventana (38°08′S, 61°47′W) in the Sierra de la Ventana, at altitudes of about 1,000 m in southern Buenos Aires Province. The habitat is one of a high pampa with flat rocks, herbaceous vegetation and small sinkholes full of rainwater. *P. casuhatiensis* feeds on beetles, spiders, and terrestrial snails (*Plagiodontes patagonicus*) (Gallardo, 1970), the latter perhaps correlated with its distinctive tooth form. According to Gallardo (1970), the populations from Cerro Tres Picos and Cerro de la Ventana exhibit slight differences in their characteristics.

Pristidactylus torquatus (Philippi)

1861 *Leiosaurus torquatus* Philippi *in* Philippi and Landeck, Arch. Naturgesch., Berlin, **27**(1): 295.—Type locality: in the neighborhood of Concepción, Chile.

1861 *Leiosaurus valdivianus* Philippi *in* Philippi and Landeck, Arch. Naturgesch., Berlin, **27**(1): 298.—Type locality: in the Province of Valdivia, Chile.

1885 *Urostrophus torquatus*—Boulenger, Cat. Liz. Brit. Mus., London, **2:** 124.

1970 *Cupriguanus torquatus*—Donoso-Barros, Bol. Mus. Nac. Hist. Nat. Chile, Santiago, **49**(24): 86.

1979 *Pristidactylus torquatus*—Montecinos Espinoza and Formas, Herp. Review, **10**(4): 121.

Diagnosis. Pristidactylus torquatus differs from the Argentinian species in having the nasal scale in broad contact with the lateral postrostral, and from the Chilean species *P. alvaroi* and *valeriae* in having more than 140 scales around midbody, and generally smaller and more numerous scales overall. Some individuals have an inconspicuous and incomplete row of slightly enlarged middorsal scales, but they are not continuous on the lumbar region as is *alvaroi.*

Distribution and Habitat. Pristidactylus torquatus occurs in forested areas of the coastal and inland cordilleras of central Chile from Curicó Province (35° 10′S) southward to southern Llanquihue Province (41° 50′S), and on Isla de Chiloé (Donoso-Barros, 1966; Formas, 1979; Montecinos Espinosa and Formas 1979). The species is arboreal, but also forages in dense brush (Donoso-Barros, 1966).

Pristidactylus alvaroi (Donoso-Barros) new comb.

1975 *Cupriguanus alvaroi* Donoso-Barros, Bol. Soc. Biol. Concepción, **47**(1974): 221; Figs. 3–5.—Type locality: Cerro El Roble, Santiago Province, Chile.

Diagnosis. Pristidactylus alvaroi differs from other members of the genus in having a markedly compressed tail, a middorsal row of enlarged scales continuous on the back, at least on the lumbosacral region, and a different color pattern.

Distribution and Habitat. The species is known only from the type locality in Chile, where it occurs in relict clusters of *Nothofagus* forest at the base of Cerro El Roble, Santiago Province (32° 58′S, 71° 01′W). It is said to be abundant (Donoso-Barros, 1975).

Pristidactylus valeriae (Donoso-Barros) new comb.

1966 *Urostrophus valeriae* Donoso-Barros, Rept. Chile, Santiago, **369:** Pl. 83. - Type locality: Alhué, Chile.

1975 *Cupriguanus valeriae*—Donoso-Barros, Bol. Soc. Biol. Concepción, **47**(1974): 223.

Diagnosis. Pristidactylus valeriae differs from Argentinian species and from *torquatus* in having fewer, larger scales all over, with fewer than 140 scales around midbody. It differs from *alvaroi* in lacking a continuous row of enlarged middorsal scales on the back, and in color pattern, and in not having a strongly compressed tail.

Distribution and Habitat. The species is known in Chile from *Nothofagus* forests of the Cordillera de la Costa near Alhué (34°09′S, 71°24′W), and from Cerro El Roble (32°58′S, 71°01′W), Santiago Province (Donoso-Barros, 1966). According to Donoso-Barros (1966) the species is not as arboreal as *P. torquatus*, and is often found in dense thickets and relict formations of *Chusquea quila*.

KEY TO THE SPECIES OF *PRISTIDACTYLUS*

1a. Scales larger and less numerous, i.e., nasal scale in broad contact with lateral postrostral; nasal in narrow contact with anterior supralabial, or narrowly separated from it by contact of lateral postrostral and anteromost loreolabial; largest supraoculars equal to or larger than scales of the supraorbital semicircles at narrowest width of frontal region; 6 to 8 scales in a horizontal line across widest part of supraorbital region between superciliaries and supraorbital semicircle; 8 to 16 scales bordering supralabials above..... Chilean species 2

1b. Scales smaller and more numerous, i.e., one or two scales interposed between nasal and lateral postrostral; nasal scale well separated from anterior supralabial by one or two scales. Largest supraoculars smaller than scales of the supraorbital semicircles at narrowest width of frontal region; 8 to 10 scales in a horizontal line across widest portion of supraorbital region between superciliaries and supraorbital semicircles; 15 to 23 scales bordering supralabials above... ..... Argentinian species.....4

2a. Scales smaller and more numerous, i.e., scales around midbody more than 140; scales bordering supralabials above more than 13; 13 to 22 scales across temporal region in a straight line from postoculars to anterior margin of ear .... *torquatus*

2b. Scales larger and less numerous, i.e., scales around midbody fewer than 140; scales bordering above supralabials fewer than 13; 10 to 14 scales across temporal region in a straight line between postocular and anterior margin of ear...3

3a. Tail more strongly compressed; a continuous row of enlarged middorsal scales on the lumbar region; dorsum greyish, venter yellow, iris red; tail conspicuously banded in adults. .....*alvaroi*

3b. Tail slightly compressed; a middorsal scale row absent on the lumbar region; dorsum bluish, venter reddish, iris blue; tail in adult not conspicuously banded; (antehumeral black mark absent in male *fide* Donoso-Barros 1966)... *valeriae*

4a. Subdigital scales distinctly multicarinate; tail less than 48% total length .... *fasciatus*

4b. Subdigital scales smooth or with one or two weak keels; tail more than 48% total length 5

5a. Subdigital scales with one or two weak keels; crowns of posterior marginal teeth somewhat swollen, the anterior and posterior cusps absent or only faintly indicated; adult male dorsal pattern a fine, dark reticulum, especially evident on the sides ..... *casuhatiensis*

5b. Subdigital scales perfectly smooth; crowns of posterior marginal teeth somewhat compressed, anterior and posterior cusps moderate or small but distinctly present; adult male dorsum nearly uniform, a fine reticulation absent 6

6a. Crowns of posterior marginal teeth flared, more strongly compressed, with larger anterior and posterior cusps; adult male uniform blue-green, green or yellow-green above ..... *achalensis*

6b. Crowns of posterior marginal teeth tapered, slightly compressed, with small anterior and posterior cusps; adult male grey or yellowish-grey above, with or without small, scattered dark spots ..... *scapulatus* 7

7a. Adult female color pattern obscure, typically broken into scattered dark spots, with dorsal cross bars faintly or not all indicated; no distinct horseshoe-shaped mark on the back of the head ..... Precordilleras and Cordilleras

7b. Adult female color pattern consisting of bold dark and light markings, a conspicuous dark horseshoe-shaped mark across the back of the head; throat and belly usually with scattered dark spots. ..... Payún, Laguna Blanca, and Canquél

ACKNOWLEDGMENTS

We are grateful to the following individuals for permission to examine specimens in their care: A. G. Kluge, The University of Michigan Museum of Zoology; H. W. Greene, Museum of Vertebrate Zoology, Berkeley; R. Sage, private collection; G. Peters and R. Günther, Zoologisches Museum der Humboldt-Universitat, Berlin; J. Cranwell, Museo Argentino de Ciencias Naturales, Buenos Aires; P. Alberch, Museum of Comparative Zoology, Harvard University; S. W. Braestrup, Zoologiske Museum, Universitetes Køben-haven; T. Cekalovic, Instituto de Zoologia, Universidad de Concepción; K. Klemmer, Natur-Museum Senckenberg, Frankfurt-am-Main; W. Ladiges and H. Koepcke, Zoologisches Museum, Hamburg; J. D. Williams, Museo de La Plata; W. E. Duellman, Museum of Natural History, University of Kansas; A. G. C. Grandison and E. N. Arnold, British Museum (Natural History); L. Castro, Instituto de Biología, Universidad Nacional de Cuyo, Mendoza; R. Braun, Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza; F. Achaval, Universidad de Uruguay; W. Hellmich and U. Gruber, Zoologisches Sammlung des Bayerischen Staates,

München; J. Guibé, Muséum National d'Histoire Naturelle, Paris; C. McCoy, Carnegie Museum of Natural History; A. Leviton, California Academy of Sciences; H. La Gilia, Museo Historia Natural de San Rafael; R. Laurent, Fundacion Miguel Lillo, Tucumán; P. E. Vanzolini, Museu de Zoologia da Universidade de São Paulo; U. Parenti, Museo Civico de Storia Naturale, Torino; J. Eiselt and F. Tiedeman, Naturhistorisches Museum, Wien; and G. Zug, National Museum of Natural History, Washington.

Funds for travel in the United States and field work in Argentina were provided by a grant from the National Geographic Society Committee on Research and Exploration. For providing laboratory facilities and access to field vehicles we wish to thank Eng. Rolando Braun, Director of the Instituto Argentino de Investigaciones de las Zonas Aridas, Mendoza, and Dr. Oswald H. Sala, Director of the Centro Nacional Patagonico in Puerto Madryn. We also thank Don Eleodoro A. Sanches, Jefe Division de la Fauna of San Juan Province for permission to work in the Reserva Provincial de San Guillermo.

We especially wish to express our gratitude to Dr. José M. Cei for his tireless efforts to make our field work in Argentina a success, and to Fernando Videla and Jorge D. Williams for their assistance in the field.

LITERATURE CITED

Barrio, A. 1969. Sobre la real ubicación genérica de *Leiosaurus fasciatus* D'Orbigny (Lacertilia. Iguanidae). Physis, Buenos Aires, **29**(78): 268–270.

Boulenger, G.A. 1885. Catalogue of lizards in the British Museum. London, **2:** xiii + 497 pp.

———. 1889. On some specimens of lizards in the Zoological Museum of Halle (Saale). Proc. Zool. Soc. London, **1889** (II): 143–145.

Bürger, O. Estudios sobre reptiles chilenos. An. Univ. Chile, Santiago, **121**(2): 147–155.

Burmeister, H. 1861. Reise durch die La Plata Staaten mit besonderer Rucksicht auf die physische Beschaffenheit und den Culturzustand der Argentinische Republik. Ausgefurt in den Jahren 1857, 1858, 1859 und 1860. Halle, **2:** iv + 538 pp.

Burt, C.A., and M.D. Burt. 1933. A preliminary checklist of the lizards of South America. Trans. Acad. Sci. St. Louis, **28**(1–2): 1–104.

Cei, J. M. 1973a. Comentarios sobre algunos géneros de iguánidos: *Diplolaemus, Leiosaurus, Aperopristis* y *Cupriguanus*. Physis, Buenos Aires, Sec. C. **32**(85): 269–276.

———. 1973b. Distribución geográfica y caracteres poblacionales de *Cupriguanus fasciatus* (D'Orbigny) (Sauria, Iguanidae). Physis, Buenos Aires, Sec. C, **32**(85): 255–262.

———. 1974. Two new species of *Ctenoblepharis* (Reptilia, Iguanidae) from the arid environment of the central Argentina, Mendoza Province. J. Herp., **8**(1): 71–75.

———. 1975. The present taxo-serological works in the field of herpetology at the Instituto Biologia Animal Cuyo University, Mendoza, Argentina. Serol. Mus. Bull., New Brunswik, **51:** 7–8.

———. 1979. The Patagonian herpetofauna, pp. 309–339. *In* W. E. Duellman, (ed.), The South American herpetofauna: its origin, evolution and dispersal. Mus. Nat. Hist. Univ. Kansas, Monog., **7:** 1–485.

———. 1980. Remarks on the taxonomic status and specific characters of *Liolaemus marmoratus* (Burmeister). J. Herp., **14**(2): 192–193.

Cei, J. M., and L. P. Castro. 1975. A serological contribution to the taxonomic status of *Cupriguanus*, a South American genus of iguanid lizards. Serol. Mus. Bull., New Brunswik, **51:** 5–6.

———. 1978a. Datos preliminares sobre las componentes de la herpetofauna de la Provincia de San Juan. Publs Occ. Inst. Biol. Anim., Univ. Nac. de Cuyo, Mendoza, Ser. Cien., **5:** 1–4.

———. 1978b. Atlas de los vertebrados inferiores de la region de Cuyo. Publs Occ. Inst. Biol. Anim., Univ. Nac. de Cuyo, Mendoza, Ser. Cien., **2:** 1–38.

Cei, J. M., and G. V. Roig. 1973. Fauna y ecosistemas del Oeste árido argentino. I. Reptiles de la Provincia de Mendoza. Deserta, Mendoza, **4:** 69–91.

di Tada, I., R. Martori, B. Kutner, and À. Ocana. 1977. Reproductive cycle and feeding behavior of *Cupriguanus achalensis* (Sauria:Iguanidae). Herp. Rev., **8**(3), suppl. p. 6.

di Tada, I., R. Martori, B. Kutner, A. Ocana, and M. Beatriz. 1977. Herpetofauna endémica de la Pampa de Achala (Córdoba, Argentina) I Reun. Iberoamer. Zool. Vert. La Rabida, **1977:** 493–512.

Donoso-Barros, R. 1966. Reptiles de Chile., Santiago, xclvi + 458 pp.

———. 1970. Católogo herpetólogico chileno. Bol. Mus. Nac. Hust. Nat. Santiago, **31:** 49–124.

———. 1975. Nuevos reptiles y anfibios de Chile. Bol. Soc. Biol. Concepción, **48**(1974): 217–229.

D'Orbigny, A. 1847. Voyage dans l'Amérique méridionale... pendant les années 1862...1833. Paris, **5**(1): 1–12; Pls. 1–15.

Duméril, A. M. C., and G. Bibron. 1837. Erpétologie générale ou Histoire Naturalle complète des reptiles. Paris, **4:** 1–572.

Fitzinger, L. 1843. Systema Reptilium. Fasciculus primus, Amblyglossae. Wien, vi + 106 pp.

Formas, J. R. 1979. La herpetofauna de los bosques temperados de Sud America, pp. 341–369. *In* W. E. Duellman (ed.), The South American herpetofauna: its origin, evolution and dispersal. Mus. Nat. Hist. Univ. Kansas, Monog., **7:** 1–485.

Gallardo, J. M. 1964. Los generos *"Urostrophus"* D. et B. y *"Cupriguanus"* gen. nov. (Sauria, Iguanidae) y sus especies. Neotropica, Buenos Aires, **10**(33): 125–136.

_____. 1967. A propósito del genero *Cupriguanus* Gallardo (Sauria, Iguanidae). Neotropica, Buenos Aires, **13**(41): 56.

_____. 1968. Dos nuevas especies de Iguanidae (Sauria) de la Argentina. Neotropica, Buenos Aires, **14**(43): 1–8.

_____. 1970. Interesante hallazgo en Sierra de la Ventana. Camping, Buenos Aires, **12:** 67–68.

_____. 1979. Composición, distribución y orígen de la herpetofauna Chaquena, pp. 299–307. *In* W. E. Duellman (ed.), The South American herpetofauna: its origin, evolution and dispersal. Mus. Nat. Hist. Univ. Kansas., Monog., **7:** 1–485.

GRAY, J. E. 1845. Catalogue of the specimens of lizards in the British Museum. London, xxviii + 289 pp.

KSOLOWSKY, J. 1895. Batrachios y reptiles de Rioja y Catamarca (Republica Argentina) recogidos durante los meses de Febrero a Mayo de 1895. Rvsta Mus. La Plata, **6:** 357–370.

_____. 1896. Sobre algunos reptiles de Patagonia y otras regiones argentinas. Rvsta Mus. La Plata, **7:** 447–457.

_____. 1898. Enumeración sistemática y distributión geográfica de los reptiles argentinos. Rvsta Mus. La Plata, **8:** 161–200.

LIEBERMANN, J. 1939. Catálogo sistemático y zoogeográfico de los lacertillios argentinos. Physis, **16**(48): 61–82.

MONTECINOS ESPINOSA, R. M., AND J. R. FORMAS. 1979. Distribution of the Chilean lizard *Pristidactylus torquatus*. Herp. Rev., **10**(4): 121–122.

MÜLLER, L. 1928. Herpetyologische Mitteilungen, Zool. Anz. **77:** 61–84.

_____. 1941. Über die in der Sammlung des Zoologischen Institutes der Universitat Halle a. Saale aufbewahrten Amphibien und Retilientypen. Zeitschr. f. Naturwiss, **94:** 182–205.

PAULL, D., E. E. WILLIAMS, AND W. P. HALL. 1976. Lizard karyotypes from the Galápagos Islands: chromosomes in phylogeny and evolution. Breviora, Mus. Comp. Zool., No. 441, pp. 1–31.

PHILIPPI, R. A., AND L. LANDECK. 1861. Neue Wirbelthiere von Chile. Arch. Naturgesch., Berlin, **27**(1): 289–301.

STEJNEGER, L. 1909. Batrachians and Reptiles, Part II, pp. 211–224. *In* W. B. Scott (ed.), 1905–1911; Reports of the Princeton University Expeditions to Patagonia, 1896–1899, Vol. III, 1, Zoology, Princeton, xiii + 374 pp.

MUS. COMP. ZOOL
LIBRARY
JUN 17 1985
HARVARD
UNIVERSITY

BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 21 JUNE 1985 NUMBER 484

MALE AGGRESSIVE BEHAVIOR IN A PAIR OF SYMPATRIC SIBLING SPECIES

JONATHAN B. LOSOS[1]

ABSTRACT. Intraspecific encounters were staged between adult male *Anolis marcanoi* and *A. cybotes* in order to describe their aggressive behavior. The major component of stationary behavior is the dewlap display, accompanied by various static and dynamic modifiers. Advancing behaviors include moving toward an opponent, threatening attack, and actual biting. The agressive behavior of *A. marcanoi* is progressive and hierarchically structured. By contrast, the behavior of *A. cybotes* is less elaborate and ritualized than that of its sibling and lacks progressive structure.

INTRODUCTION

Defined simply as "pairs or even larger groups of related species which are so similar that they are considered as belonging to one species until a more satisfactory analysis clears up this mistake," (Mayr, 1942) sibling species have been discovered at an increasing pace as the level of systematic analysis has become finer, passing from examinations of morphological characters to investigations of molecular properties.

The different patterns of distribution of sibling species raise interesting ecological questions. On one hand, sibling species may be completely allopatric, which raises questions more about the evolutionary forces operating to produce such species than about the

[1]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. Present Address: Museum of Vertebrate Zoology and Department of Zoology, University of California, Berkeley, California 94720.

ecological relationships between them. On the other hand, parapatric and sympatric sibling species distributions bear directly on ecological theory. In theory, two species occupying the same niche cannot long coexist unless differences sufficient to lessen competitive pressures evolve. The parapatric ranges of many sibling species pairs or groups attest to the difficulty such species have in coexisting (e.g., the members of the *Rana pipiens* complex in North America [Pace, 1974] and the *Anolis chlorocyanus* [Williams, 1965] and *A. ricordii* [Schwartz, 1974] groups in Hispaniola). One would expect that sympatric sibling species would exhibit differences in morphology, physiology, or behavior that would permit coexistence. Indeed, resource partitioning of some kind is observed in almost all known cases of sympatric sibling species (Mayr, 1942; Schoener, 1977).

In this regard, the curious case of the Hispaniolan sibling species *Anolis cybotes* and *A. marcanoi* warrants attention. *Anolis cybotes*, the larger of the two, is found throughout the island, while *A. marcanoi* is restricted to a small area in the southwest portion of the Dominican Republic (Williams, 1975). The two are classic sibling species, consistently separable morphologically only by the color of the dewlap of males and the throat of females: *Anolis marcanoi* has a red dewlap or throat, while that of *A. cybotes* is usually either white or yellow, depending on locality (Williams, 1975). Electrophoretic studies by Webster (1975), however, clearly reveal that the two are distinct species. Table 1 provides a review of differences between the species.

Ecologically, the species are just as similar. Unlike the cases of sibling species already discussed, no apparent differences in physiology or microhabitat preference have been discovered. They are patchily sympatric throughout the range of *A. marcanoi* and have been noted on adjacent fenceposts in some areas (Hertz, 1980), while in other locations only one species is present. Hertz suggests that *A. marcanoi* may be better adapted for hotter, more open microhabitats, but no consistent differences have been noted in the field (Williams, 1975; Hertz, 1980; personal observation).

At issue is the manner in which these species interact. Are the differences between the species in dewlap color sufficient to allow species recognition, or are there also behavioral differences of importance? If species recognition is highly accurate, do the similar-

Table 1. Differences between *Anolis marcanoi* and *Anolis cybotes*.*

	A. cybotes	*A. marcanoi*
range	widespread throughout Hispaniola	Peravia Province, southwest Dominican Republic
dewlap color	normally white to yellow, except some populations on the extreme end of the southwestern peninsula in Haiti, which are red	red
scale characters	middorsal and midsacral scales sometimes enlarged	middorsal and midsacral scales rarely enlarged
maximum snout-vent length	81 mm	65 mm
heat tolerance: Experimental Voluntary Maximum	34.3° C	35.7° C
Critical Thermal Maximum	38.4° C	40.5° C

*After Williams, 1975 and Hertz, 1980.

ities between the species lead to resource competition and interspecific aggression? The goal of this study is to provide a thorough description of intraspecific male aggressive behavior in the two species. In themselves, reports on the intraspecific male aggressive behavior of both species are important because detailed characterizations of the components and progression of male aggressive behavior in *Anolis* are not common (the only reports of comparable detail are Greenberg and Noble, 1944, and Greenberg, 1977, on *A. carolinensis* and Jenssen 1979a and 1979b on *A. opalinus*). Furthermore, in order to analyze interspecific interactions, it is first necessary to understand the dynamics of intraspecific behavior. This knowledge then may be used as a control with which interspecific aggressive behavior can be compared.

MATERIALS AND METHODS

In January 1983, adult male *A. marcanoi* were collected past the first ford on the El Recodo road, approximately 6 to 10 km north of

Bani, Peravia Province, Dominican Republic. Adult *A. cybotes* were collected at that locality and in Santo Domingo, Dominican Republic. The lizards were housed in terraria in the Biological Laboratories, Harvard University, and provided with perches, small potted plants, and a soil substrate, and offered several crickets one to two times a week and water three to four times a week. Room temperature was maintained at approximately 26 to 30° C. Individuals were separated from other males in the same terrarium by cardboard partitions.

Encounters between two conspecific males were staged between 23 March and 16 December 1983. Lizards were placed in the partitioned halves of either a 41 × 22 × 20 cm (the first 14 *A. marcanoi* encounters) or a 74 × 32 × 29 glass terrarium (the last 12 *A. marcanoi* and all 19 *A. cybotes* encounters) covered with a mesh lid and provided with perches in each half of the terrarium. Lizards were left undisturbed in the terrarium for a period ranging from 17 hours to four days, but usually lasting two days. Water was only provided when an encounter had to be postponed, forcing the period to exceed two days. Lizards were allowed to acclimate in order to gain familiarity and enhance territorial defense.

Approximately 15 to 30 minutes prior to an encounter, a 250 W infrared light was switched on, warming the terrarium to 25 to 32° C and markedly increasing the activity level of the lizards. Temperature in the room in which the encounters were staged was approximately 20° C.

Encounters were initiated by lifting the partition. All lights in the room were extinguished, except two 60 W desk lamps pointed directly into the terrarium which lit the display arena and made it difficult for the lizards to see observers in the room. Encounters were videotaped on a Panasonic NV-8050 time lapse recorder with a MTI-65 video camera and a Canon 16-100 mm TV zoom lens and then analyzed at normal and slow-motion speeds on a Panasonic WV-5350 video monitor. Encounters normally lasted 45 minutes, but were terminated when one lizard tried repeatedly to escape from the other, and were extended when the lizards were still intensely interacting at the end of the alloted time.

Twenty-one *A. marcanoi* and ten *A. cybotes* were used in these encounters. Lizards were paired randomly, with the constraints that they had not been housed in the same terrarium, that they had no

prior experience with each other (two exceptions), and that there was no more than a 5 mm difference in snout-vent-length.

RESULTS

The aggressive behavior of the lizards can be divided into two categories: stationary and advancing behavior. In stationary behavior, the lizard remains in one area and primarily moves its head, bobbing with or without extension of the dewlap. Several modifiers of this display, either morphological changes or movements of body parts, are correlated with aggressive intensity, particularly in *A. marcanoi*. The level of intensity of *A. marcanoi* could be judged by the correlated appearance of behavioral and morphological responses. As displays progressed, lizards generally displayed a sequence of actions and display modifiers, adopted a more threatening posture with body and head raised and apparent size maximized, and became more active. By contrast, in *A. cybotes* there was little correlation between the appearance of particular aspects of aggressive behavior. Thus, level of intensity was more difficult to gauge.

In advancing behavior, the lizard moves toward its opponent. In the early, less intense stages, the lizard makes various intention movements, while later stages involve lunging and biting.

The male aggressive behavior of the two species differed in two major respects. First, though elements of both stationary and advancing behavior were displayed by *A. cybotes*, many of the components of these behaviors were absent or much less elaborate than those exhibited by *A. marcanoi*. Second, the ordered appearance of progressively more aggressive behaviors, so integral a part of male-male interactions of *A. marcanoi*, was absent in the behavior of *A. cybotes*. In most cases, particularly among stationary behaviors, any particular behavior did not necessarily follow any other particular behavior, nor did particular behaviors connote different levels of aggression.

Stationary Behavior

The primary stationary display of the lizards was the dewlap display, composed mainly of head-bobbing and dewlap extension.

Dewlap Display

Anolis marcanoi

There were generally three levels of intensity of the display exhibited by *A. marcanoi*. Intensity is best correlated with the degree to which the lizard elevated its body above the substrate.

The *low level dewlap display*, often the first display the lizard would make in an encounter, involved little body elevation. The body occasionally remained completely in contact with the substrate, but usually the anterior portion of the body was slightly lifted by extending the front limbs, holding them out to the side in the typical reptilian stance (Fig. 1a). The result was that the forequarters were raised several mm off the substrate. The snout was also angled upward at 30 to 45 degrees to the ground. The head usually was kept in the vertical plane of the body. During the process of raising the body and snout, the dewlap usually was extended completely with several rapid head bobs. On a number of occasions, the forebody distinctly raised first, and then the dewlap extended, but the two usually occurred simultaneously.

This display occurred primarily at the start of an encounter, shortly after the partition had been raised, though sometimes it was omitted altogether. Occasionally, when an encounter had proven indecisive and the lizards had calmed, they would revert to this level.

The *intermediate dewlap display* involved an increase in body elevation. Generally, it took one of two forms: either the forelimbs were completely extended with the snout pointed at a very high angle (75 to 90 degrees), giving the whole body a very steeply sloped configuration, or all four legs pushed up, with the hind legs out to the side, elevating the whole body off the substrate (Fig. 1b). The tail was then usually also lifted, either held rigid and completely elevated, or slightly arched with the posterior half dropping to the substrate. The tail was also on occasion held higher than the body or was even curled back above it. The dewlap was extended completely in this display; the snout's higher angle and the higher elevation of the forequarters (at least a little higher in the second variation than in the low level dewlap display) allowed the dewlap to be lifted completely off the substrate.

In the highest level of intensity display, clearly distinct from the first two, the entire body was elevated high off the substrate (Fig. 1c). In the *full elevation display*, the forelimbs were held under the

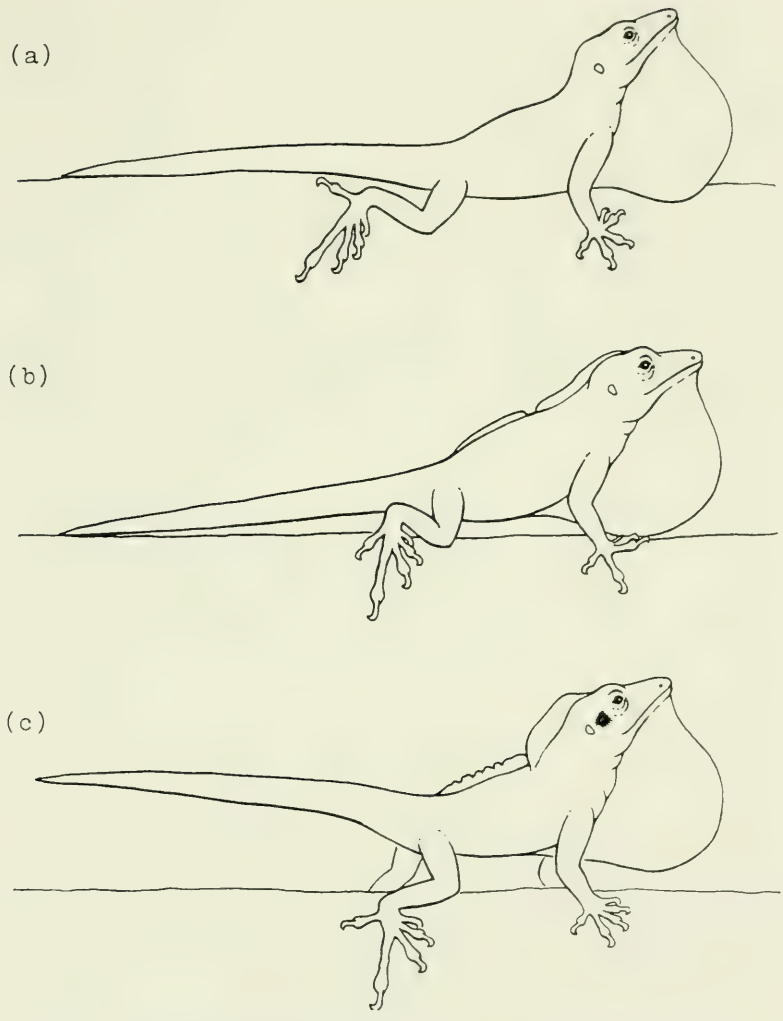


Figure 1. Male *Anolis marcanoi* performing (a) low-level, (b) intermediate, and (c) full elevation displays. Display modifiers shown here, such as crest erection and head spot darkening, were noted in all three display levels, through they were more common in the more aggressive levels.

body and almost completely straightened, while the hindlimbs were pushing up greatly either sprawled out to the side or also under the body. The tail was usually rigidly held straight back or even held higher than the body. The snout was very high, and the dewlap was well off the substrate.

Several particular aspects of the display varied independently of these levels, though in some cases relationships were noted. The most variable, and perhaps most significant, component of the display involved the dynamics of dewlap extension. In general, the degree of extension varied as a function both of time elapsed and intensity of the encounter. The dewlap was usually completely extended and maintained or pulsed (retracted and reextended) to a barely perceptible extent at the beginning of encounters and when a high level of intensity was observed. As encounters progressed into series of alternating exchanged displays, dewlap extension tended to decrease both in extent and duration. Often, the dewlap would only be pulsed out briefly at the end of a series of bobs; the amount of dewlap extended varied similarly, sometimes only revealing a slight bit of the dewlap, and sometimes not at all. If intensity increased, for example as a result of an advance by one of the lizards, dewlap extension would increase in subsequent bobbing.

Anolis cybotes

Anolis cybotes only has one level of dewlap display, comparable to the *low level dewlap display* of *A. marcanoi*. A lizard displayed with its posterior half in contact with the substrate, while its anterior was raised a variable amount by extension of the forelegs (Fig. 2), either out to the side or directly under the body. The snout also was angled upward to a variable degree. On rare occasions, usually when it was on the ground, a lizard displayed with all four legs out to the side, pushing its body up off the ground.

The dewlap was usually extended, at least in the initial bout of displaying, with concurrent head-bobbing. The amplitude, number, and even presence of bobs varied. On occasion, usually later in an encounter, the dewlap was extended and retracted without any head movement at all. As with *A. marcanoi*, sometimes the dewlap was extended and then retracted, while other times it was maintained at full extension.

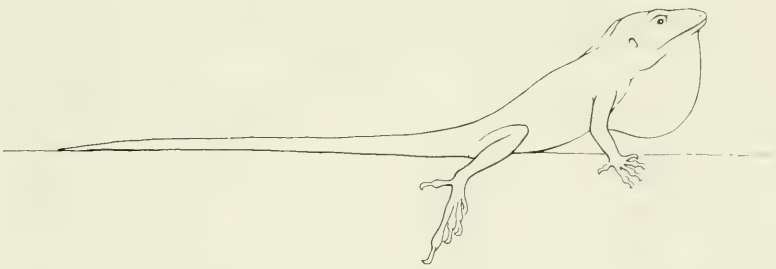


Figure 2. Typical display posture of male *Anolis cybotes*. The forequarters are elevated, but the hindquarters are firmly planted on the substrate. The nuchal crest is occasionally erected more fully, and the dorsal crest is sometimes apparent. The dewlap often is extended more fully.

Head Bobbing

Anolis marcanoi

Though the bobs of the head usually were part of the dewlap extension process, similar to the fanbob of *A. aeneus* (Stamps and Barlow, 1973), in later stages of the encounter, especially when the lizards were alternating displays, the bobs were increasingly emphasized and independent of dewlap extension. A series of 2 to 10 bobs, either of the normal amplitude or greatly exaggerated with several times that amplitude, were performed without dewlap extension, or as a distinct precursor to extension. At other times, the dewlap was pulsed out with exaggerated jerking bobs, similar to the jerkbob of *A. aeneus*. The lizards sometimes bobbed several times at full dewlap extension, with a slight pulse of the dewlap during each bob and slight retractions in between. This usually occurred when the display intensity was high. In several cases, a subordinate lizard raised and lowered its head extremely slowly with large amplitude and no dewlap extension. This was usually repeated several times.

Jenssen (1983) found that *A. cybotes* performed only one stereotyped head bobbing pattern, in contrast to the greater repertoires of other *Anolis* (Jenssen, 1977, 1978). A detailed investigation was not conducted, but from an analysis of the diplays of several lizards, it appears that *A. marcanoi* has at least two distinct display types. However, neither the extent of variation nor the degree of stereotypy of the head-bobbing patterns were determined. It is possible

also that *A. marcanoi* has several other head-bobbing patterns that were not discovered. No relationship between level of dewlap display and head-bobbing pattern was found.

In the first pattern, equivalent to the signature display (Stamps and Barlow, 1973; Jenssen, 1978), the head was bobbed once or twice with great amplitude, often with a pause in between bobs, and then rapidly bobbed another 7 to 17 times with the snout remaining elevated (Fig. 3). The dewlap began to expand between bobs six to nine, at which time the bobbing would begin to slow. Several times this display was prefaced with a lowering and raising of the head, akin to, though slower than, the "head-dipping" of *A. cybotes* (Jenssen, 1983). Jenssen (personal communication) pointed out the close similarity between this display pattern and the sole one reported for *A. cybotes*. Only the number of initial large-amplitude bobs—one or two in a *A. marcanoi*, three in *A. cybotes*—distinguishes the two, attesting to the close relationship of the two species. This pattern was observed most often early in encounters, though it was also seen sometimes at high levels of intensity. This description must be considered tentative, however, because it is based on only four displays of three lizards.

A second display, probably functioning as a challenge display (Jenssen, 1978), was often seen late in encounters, especially when lizards were fairly close to each other and alternating displays. It was characterized by a large amplitude dip of the head, a pause, and then three or four rapid low amplitude bobs with the head not quite

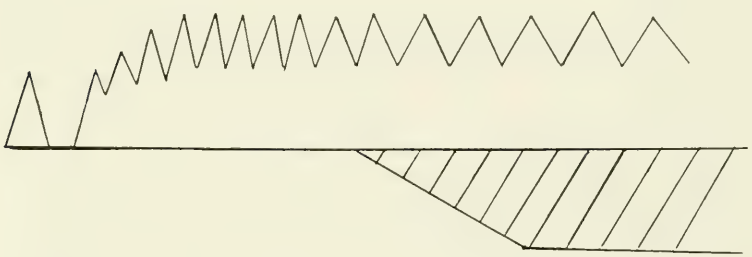


Figure 3. Sample display-action pattern graph of the first head-bobbing pattern of *Anolis marcanoi*. The line represents approximate elevation through time. The shaded region represents dewlap extension through time. This pattern was sometimes preceded by a dip of the head.

dropping back to its original level (Fig. 4). Sometimes, there was a pause after the bob, with the head often not returning to its original level. Usually the dewlap was brought out only at the end of the bobbing sequence, if at all. This description is based on an analysis of nine displays by four lizards. It did seem to be fairly stereotyped, however, and was observed in the displays of many of the other lizards.

Intensity was reflected in the length and magnitude of dewlap display and head-bobbing. More intense encounters tended to have longer displays with greater number of bobs and pulses and greater dewlap extension. The pace of the displays was also faster in more intense displays. If these intense encounters did not immediately progress into more direct aggressive action, however, displays tended to become shorter and less animated, often devolving into the alternating bouts of medium speed bobbing mentioned above.

Anolis cybotes

Because Jenssen has already extensively examined the stereotyped head-bobbing patterns of *A. cybotes*, they were not investigated here. Two distinct methods of bobbing were noted in *A. cybotes*. In one, by far the more common in *A. marcanoi*, the whole head was bobbed, passively moving the dewlap along with it, but without greatly changing its amplitude. This method of bobbing produces the head-bobbing display action patterns so extensively studied in *Anolis*.

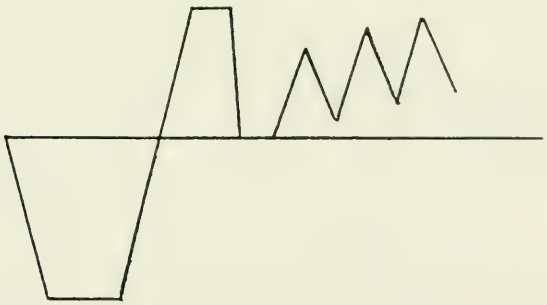


Figure 4. Sample of the second head-bobbing pattern of *Anolis marcanoi*. Though not indicated here, the dewlap was occasionally extended at the end of the display.

By contrast, dewlap bobbing—rarely exhibited by *A. marcanoi*, but commonly performed by *A. cybotes*—primarily involved moving the dewlap up-and-down by raising and lowering the posterior portion of the hyoid, causing a large amplitude change in the dewlap, but moving the head only slightly. This bobbing type was usually preceded by the first type and appeared when the lizard was displaying intensely. Only the first type was involved in dewlap extension.

The quick inverted head bob or "head dip" noted in wild *A. cybotes* by Jenssen was observed on a number of occasions. His observation that head dips were often performed independently of dewlap displays was confirmed, though no long series of head dips, which Jenssen also reported, were noted in these experiments.

Static Modifiers

Several morphological responses—Jenssen's static modifiers (Jenssen and Hover, 1976; Jenssen, 1977, 1978)—were also indicative of level of intensity, particularly in *A. marcanoi*.

Anolis marcanoi

Both the nuchal and dorsal crests were often erected during displays (Fig. 1b, and 1c). Often, they were erected, retracted, and erected again several times in an encounter. The nuchal crest always appeared before and disappeared after or simultaneously with the dorsal crest. The crests often at first were erected fully, but then retracted to only a fraction of their full size as the encounter continued.

The presence of fully erected crests indicated a high intensity state, but their absence did not imply the converse. When the distance separating the lizards was not great, actions more aggressive than the *full elevation display* were generally accompanied by full crest erection, as were most *full elevation* and some *intermediate elevation displays*. Crests were noted less frequently when the lizards were displaying from across the large terrarium. Lizards that appeared clearly subordinate—indicated by display level, activity, posture, and, retrospectively, by the outcome of the encounter (see below)—were much slower to raise their crests and maintained them generally for a shorter period.

Similarly, the appearance of a dark spot on the side of a lizard's head correlated broadly with intensity. Between the eye and the tympanic opening, a black circular spot slightly larger than the tympanic opening would appear when a lizard was aroused (Fig. 1c). A similar well-defined dark patch with a similar function has been reported for *A. carolinensis* (Greenberg and Noble, 1944; Greenberg, 1977), but in that species the patch is rectangular and directly postorbital without intervening undarkened scales. The appearance of the spot in both species seems clearly a function of arousal; lizards handled during transfer to and from the experimental arena almost invariably exhibited it and often tried to bite. Many other *Anolis* display an irregular darkening in that region when aroused (G. C. Mayer, personal communication; personal observation). Dominant lizards were much more likely to exhibit the spot than subordinate ones, which rarely displayed it except at the highest levels of intensity, and only then when putting up resistance instead of fleeing. As with the nuchal and dorsal crests, black spots were usually apparent, especially on dominant lizards, at high levels of intensity, and sometimes at lower levels, ranging from *low level dewlap displays* to *full elevation displays*. Darkening of the spot almost invariably was preceded by erection—though not necessarily full erection—of the crests. As with crest erection, the spot appeared much more frequently when the distance separating the lizards was not great.

Body orientation and appearance also were important components of the display. Lizards, especially dominant ones, increased their apparent body size several ways. The apparent size of the head was increased by erecting the nuchal crest, engorging the head, and lowering the hyoid apparatus of the throat. Such enlargement is a common aggressive response in iguanids (Greenberg and Noble, 1944; Carpenter, 1967). Presumably, dewlap extension has the same effect of making the lizard appear larger. When retracted, the dewlap remained apparent, ranging in size from a slight rim to a fairly large crescent, making the head region appear larger. The body was also made apparently larger by expansion of the dorsal crest and lateral compresion of the body. Subordinate lizards, as well as dominant lizards displaying after winning an encounter (indicated by quiescence or flight of their opponents) rarely attempted to increase their apparent size.

Lizards also attempted to assume a position that would expose the greatest part of their bodies to the other lizard, increasing their apparent size. When both lizards were displaying, the most common position was a parallel alignment, each lizard exposing its broadside to the other. As with many other *Anolis* (e.g., Carpenter, 1965, 1967), when not aligned parallel, one or both lizards (usually the one with less apparent broadside exposure to the other) would turn its head, so that the dewlap when extended would be parallel to the other's head and thus appear as large as possible. Maximizing apparent size was most obvious when one lizard was on a perch while the other was nearby on the ground. In these instances, displaying in an upright position on the branch would not present as large an image as possible to the lizard on the ground. Invariably, the lizard on the branch would display on the side of the branch. The closer the lizard on the ground was to the branch, the greater would be the angle from the vertical of the lizard on the branch. When the lizard on the ground was directly underneath the branch of the other lizard, the latter would arrange itself horizontally, at a 90° angle from the upright. By contrast, a lizard displaying to another lizard also on a perch would always display directly upright on the perch.

Anolis cybotes

As with *A. marcanoi*, several morphological responses were noted as part of the male-male interactive behavior of *A. cybotes*. In the latter species, however, lack of a particular static modifier—or of all static modifiers—did not necessarily correlate with low levels of intensity.

Like *A. marcanoi, A. cybotes* possesses both a nuchal and a dorsal crest. The crests appear to be smaller in *A. cybotes* and are fully erected much less frequently. Often, the dorsal crest was visible only as a low ridge along the lizard's back. Crest erection appears to serve the same function in both species, increasing apparent size and indicating heightened level of intensity. In the eight encounters in which dominance could be determined (with *A. cybotes*, dominant lizards could only be determined post facto; dominance could not be determined by the presence of hierarchically higher displays and modifiers as it could with *A. marcanoi*), five of the dominant lizards displayed crest erection. In two of the three other instances, no other

preliminaries to a direct attack occurred. Only two of the eight subordinate lizards displayed crest erection, both in encounters in which the dominant lizard also displayed crest erection.

Anolis cybotes does not have a well-defined circular head spot like that of *A. marcanoi*. It can, however, change skin hue (as can *A. marcanoi*); often, dominant lizards became lighter. An ill-defined darkening of the skin in the postorbital region of the head, where the dark spot in *A. marcanoi* is located, was noted on several occasions, usually when the lizard was aroused by another male or was handled. Only in one lizard, however, was anything approaching a circular spot apparent.

As with *A. marcanoi, A. cybotes* attempted to increase its apparent size in various ways. This was observed more often in dominant lizards, though in some cases both lizards attempted to increase their size. Apparent size was increased in several ways, all also exhibited by *A. marcanoi*. Most common, other than dewlap extension, was enlargement of the head. Lizards also increased their apparent size by lateral compression and throat enlargement.

Dynamic Modifiers

Several display modifiers involved moving body parts and thus constituted dynamic modifiers (Hover and Jenssen, 1976; Jenssen 1977, 1978). Instead of bobbing with the head, on several occasions lizards raised and lowered the body by pushing up with the legs, primarily the forelegs. Push-ups have been widely reported among *Anolis* (e.g., Greenberg, 1977; Jenssen, 1979a), and iguanids in general (Carpenter, 1967), but no correlation with intensity was discovered in *A. marcanoi* or *A. cybotes*.

Anolis marcanoi

The *full elevation display* was the most active level of dewlap display. The rear of the body was moved independently in several ways. Most common were push-ups with the rear legs, usually in series of two to six causing the posterior to oscillate greatly, similar to "rearing" observed in *A. opalinus* (Jenssen, 1979a). The precursor of these pelvic push-ups could be seen in several *intermediate dewlap displays* in which the rear legs were raise and lowered slightly as the dewlap was thrust out during head-bobbing. In the *full elevation display*, the lizards also sometimes jumped backwards

several times in rapid succession, forcing the posterior of the body up-and-down in a manner similar to that caused by hind-leg push-ups. Similar behavior in the same context has been noted in male *A. lineatopus* (Rand, 1967). The *full elevation display* was usually only performed in response to a dewlap display or other action by the other lizard in an encounter. Posterior movements were never performed without such provocation.

Head orientation was also related to intensity level. Throughout the dewlap displays, and especially at low intensity levels, lizards changed their head orientation frequently and usually rather slowly. The snout was often pointed at the other lizard, but this action in itself did not seem highly significant. On the other hand, a lizard rapidly turning its snout toward the other, either at the end of a display by the former or during the display of the latter, appeared to indicate a high level of intensity. Generally, pointing occurred during *intermediate* or *full elevation displays* or more intense behavior and was more often performed by the dominant lizard in the encounter. When a dominant lizard rapidly pointed its snout at a displaying subordinate lizard, the latter often ceased its display, retracted its dewlap, and dropped to a less elevated posture.

Anolis cybotes

There was no indication in *A. cybotes* of anything resembling the pelvic push-ups of *A. marcanoi*. The posterior was always stationary and usually firmly on the substrate, though occasionally the entire body was lifted off the substrate.

Pointing with the snout at an opponent was commonly seen in *A. cybotes*, though neither as frequently nor in as defined a manner as in *A. marcanoi*. Several times, a lizard rapidly turned, its snout and even its whole body directed at its opponent, briefly paused, and then leapt at or toward it. The derivation of pointing in *A. marcanoi* may thus be revealed; perhaps pointing in *A. marcanoi* has become ritualized, detached from its original threat of imminent attack. Pointing was never observed by a lizard which would subsequently lose an encounter.

A common action more frequently displayed by *A. cybotes* than by *A. marcanoi* was tilting or cocking the head downward toward an opponent. This often occurred when the lizard was on a branch, looking down upon an opponent on the ground and often was

associated with some movement or action by the other lizard. Though cocking of the head may simply allow better vision of the other lizard's actions, it probably has a communicative function, perhaps as an intention movement, indicating awareness of the other lizard's actions and readiness to respond. *Anolis* also commonly performs this behavior prior to attacking potential prey items (G. C. Mayer, personal communication). Dominant lizards more commonly performed this behavior.

Advancing Behavior

Past the stationary display, the steps of increasing intensity of aggression become more stereotypical, involving movement toward an opponent and threat of or actual attack, though often interrupted by more bouts of unilateral, alternating, or simultaneous dewlap displays. In most cases, the progression to increasing levels of intensity was only stopped by fleeing or quiescence of the subordinate lizard, particularly in *A. marcanoi*, though several times both lizards ceased behaving and assumed less intense postures without either clearly "winning" the encounter.

Anolis marcanoi

Figure 5 presents the flow of advancing behaviors of *A. marcanoi*.

Rapid pointing of the snout toward the other lizard was the lowest level of advancing behavior as well as a display modifier, though it was still usually tied to the interspersed dewlap displays.

Taking one or several steps toward the other lizard is the first overt threat of attack. At close proximity, stepping toward the other lizard threatened imminent attack and often caused the other lizard to cease its display and/or assume a more subordinate position, retreat one or several steps, or seek escape from the encounter.

Also at closer proximity, intent, or at least threat, to attack was indicated by the assumption of a "poised" position. The body was held off the ground with the legs out to the side and appearing ready to spring. The head, enlarged by crest and throat expansion, with the dewlap not usually greatly extended, was tilted somewhat forward and toward the other lizard. Rarely was this position assumed without a subsequent attack. At this time, the lizards were usually in the faceoff position (Carpenter, 1962, 1978), their bodies parallel with heads pointed in opposite directions. When displaying on a

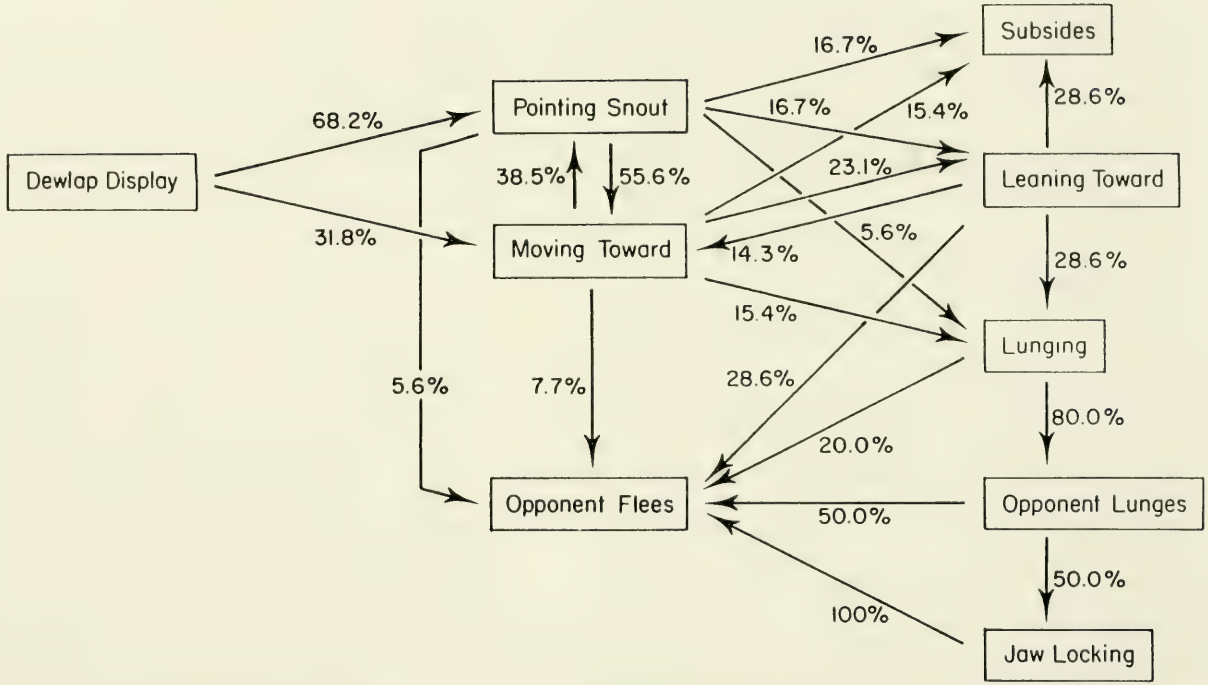


Figure 5. Flow of the behavior of the 22 *Anolis marcanoi* that exhibited advancing behavior. Advancing behavior was always preceded by dewlap display. Dewlap displays and behaviors that occurred more than once most notably repeated snout pointing were scored only once. Lunging is only scored for the lizard which initially lunges. Lunges by the second lizard fall into the category of "opponent lunges." Similarly, fleeing is only recorded in "opponent flees." Consequently, output does not always equal input for a box.

perch, this poised position often took the form of a crouch, clearly threatening a jump toward the other lizard. Echelle et al. (1971), in a study of aggressive behavior in nine Costa Rican *Anolis*, noted the assumption of a similar position in males that subsequently attacked their opponents.

Usually following the poised position was an advance toward the rear of the other lizard, culminating in an open-mouthed lunge toward the other lizard's hindquarters. Biting was never observed at this stage. Often the tongue was bunched at the front of the open mouth. Though tongue-bunching is characteristic of aggressive interactions in many *Anolis* species (e.g., Greenberg, 1977), it does not appear to have consistent importance in *A. marcanoi*. Attacking individuals always lunged with mouth open and often kept the mouth open while displaying after lunging. In addition, two lizards opened their mouths in threat displays without immediately lunging afterwards.

The attacked lizard responded either by jumping back and fleeing, or pivoting, usually with a jump backwards, away from the attacking lizard, with its head turned over the shoulder toward the attacking lizard. The two lizards, now in semi-circular positions with heads at opposite ends, displayed at each other, bodies completely elevated off the ground and snouts angled up, with mouths, at least initially, wide open. Occasionally, the attacking lizard continued moving toward the other's rear so that both circled around, maintaining the same relative position. In several instances, the attacked lizard, after displaying, lunged for the other's rear, though in no instance was it successful in driving the former off. In all but two cases, after a sequence of displays, lunges, and circling motions, the attacked lizard fled and attempted to escape the terrarium by running to a distant wall and clawing wildly at it.

In two instances, the two lizards locked jaws for less than two seconds, shaking each other violently, until they released, jumping backwards, with the attacked lizard fleeing. In one of these instances, the attacking lizard chased the other lizard several steps before ignoring it.

In all instances in which the losing lizard fled, the winning lizard continued displaying for up to several minutes. Slowly, the lizard's displays and postures descended the stages of intensity, though they would temporarily reascend if the other lizard came nearby in its

attempts to escape the terrarium. Ultimately, the winning lizard would assume a non-aggresive posture, stretched out on a perch or the ground with its head on the substrate or barely elevated and its rear legs stretched back behind it. The overall effect was to increase its length while decreasing its apparent height. This is the normal resting position of the lizards when undisturbed.

Anolis cybotes

Advancing behavior was progressively ordered to an extent, but not completely (Fig. 6). In the most structured sequences, a lizard performed some display behaviors and then moved towards its opponent, either jumping off a branch or running half or more of the distance separating the lizards. This was usually done at a rapid pace. The advancing lizard then adopted a stalking, "poised" position, somewhat like that exhibited by *A. marcanoi*, but with all four legs out to the side, seemingly prepared to spring, with the long axis of the body pointed directly at the other lizard. This was not always seen, and sometimes a lizard hardly paused between moving toward and actually attacking the other lizard.

The act of biting an opponent was very different in the two species. Encounters involving *A. marcanoi* only resulted in biting when both lizards continued to behave intensely. The sequence of faceoff position-lunging-biting was seen only once in the *A. cybotes* encounters. Instead, most incidents of biting involved very little ritualized behavior. One lizard leapt or ran at the other and bit it behind the head, attempting to pin it to the substrate. Attempts to escape by the attacked lizard often resulted in that lizard carrying the other around on its back. The attacked lizard often was not displaying vigorously and in several cases was trying to escape from the attacking lizard. *Anolis marcanoi* rarely exhibited chasing behavior, but this was common in *A. cybotes*. In the latter species, on occasion, lizards were chased all over the aquarium until they could be cornered and bitten.

Most surprising were two instances in which a lizard, with no preliminaries, ran directly and rapidly at the other lizard, which also had exhibited no aggressive behavior, and bit it behind the head. In both cases, the attacking lizard persistently bit and chased the other lizard until the encounter was ended. This was reminiscent of the "vicious biting attack" termed "abnormal" by Greenberg and Noble

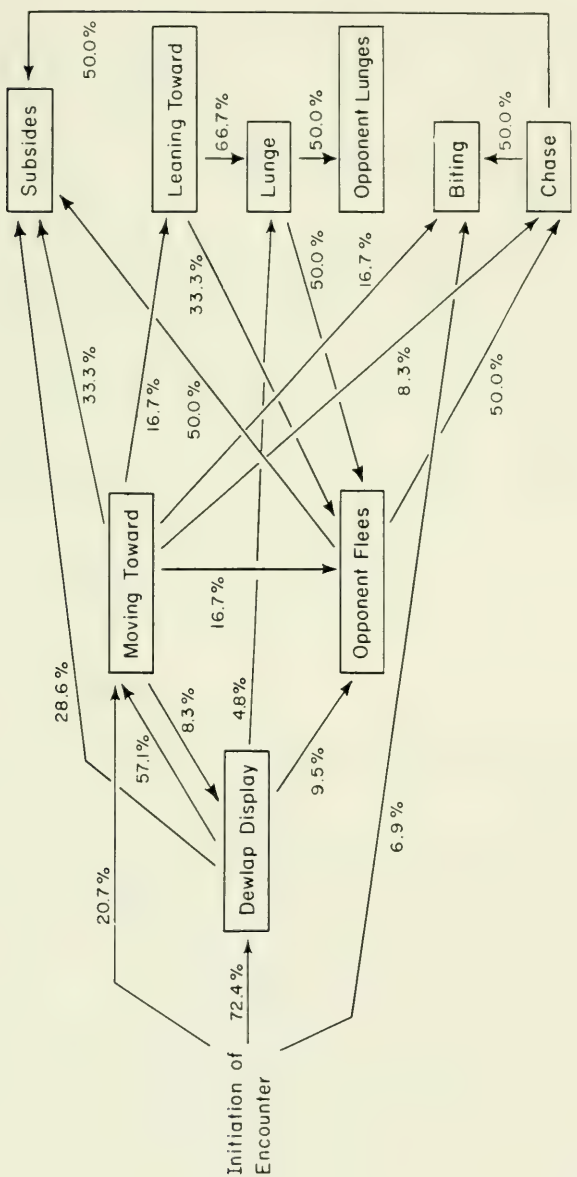


Figure 6. Flow of aggressive behavior of *Anolis cybotes*. See Figure 5 for details of flow chart construction.

in *A. Carolinensis* (1944). This behavior was observed by these investigators in 18 or 800 males, as well as in some females and surgically-altered males.

Submissive Behavior

Anolis marcanoi

As indicated previously, subordinate individuals usually did not posture as intensely as dominant lizards. Dewlap displays were generally less elevated, shorter in duration, less frequent, and often without crests or dark spots. Subordinate lizards also did not as often attempt to enlarge their apparent head or body size.

More submissive behavior generally took the form of staying very low to the ground, with the head elevated little and the snout angled up only slightly, if at all. Carried to the extreme, completely submissive lizards laid completely flat on the ground, appearing as inconspicuous as possible.

At higher levels of intensity, particularly in response to advancing behavior, submissiveness was usually indicated by fleeing the encounter and attempting to escape the aquarium.

Anolis cybotes

One of the most surprising aspects of *A. cybotes*' behavior is the lack of submissive behavior in the lizards that were judged, by the eventual outcome of an encounter, to be subordinate. Unlike *A. marcanoi*, these lizards did not behave less vigorously or aggressively, nor did they necessarily display fewer behaviors connoting higher levels of intensity than the dominant lizard in the encounter. In several cases, the subordinate lizard initiated aggression by moving toward the other lizard. This was never seen in the *A. marcanoi* encounters.

More generally, lizards did not adopt a submissive posture as *A. marcanoi* did. They sometimes moved away or displayed less, but they did not flatten themselves or otherwise appear inconspicuous. Often, a lizard appeared to be trying to escape the aquarium, though neither persistently nor frantically enough to warrant ending an encounter. When this proved futile, the lizard turned back and behaved aggressively again toward the other lizard. Such behavior was rarely exhibited by *A. marcanoi.*

Index of Aggression

In order to quantify levels of intensity in interactions, an index of aggression, similar to that developed for Puerto Rican anoles by Ortiz and Jenssen (1982) was constructed. The index assigns progressively higher point values for actions indicating greater intensity (Table 2). This index, then, can be used to compare quantitatively the level of aggressive intensity of *A. marcanoi* in inter- and intraspecific encounters (Losos, in press). Points for any behavior are scored only once per encounter even though many behaviors are repeated periodically. The score of a lizard in an encounter is the sum of points awarded for behaviors which it exhibited.

The behavior of *A. marcanoi* was progressive, with the less aggressive behaviors preceding the more intense ones. Because this was not the case for *A. cybotes*, no index of aggression could be developed for that species. Occasionally, the actions of *A. marcanoi* during the dewlap display did not necessarily follow a set hierarchy of increasing intensity either. The most notable exception occurred when a lizard, usually at a distance from its opponent, sometimes moved toward the other before pointing its snout rapidly and directly at it.

Table 2. Index of Aggression used to score encounters between adult male *Anolis marcanoi*.

Points	Action or Display Modifier
1	low level and intermediate dewlap display
2	full elevation dewlap display
2	crests erected
3	head spot apparent
3	lifting the pelvic region and/or moving backwards during dewlap display
3	pointing snout rapidly at opponent at conclusion of own display or during opponent's display
4	moving toward opponent (including jumping onto or off of perch)
6	adopting poised position
7	lunging toward opponent
8	locking jaws
8	opponent flees

Several notes on the construction of this index are necessary. Only two levels of dewlap display are scored although three were recognized. The *intermediate dewlap display* stage was considered only slightly more intense than the *low level dewlap display*, and consequently the two were grouped together. Though the nuchal crest is almost always erected before and retracted after the dorsal crest, they are not considered independent behaviors denoting different levels of aggressive intensity. The scores of the lizards agree well with the qualitative evaluations of the 26 encounters. The encounters can be split into four categories based on their outcome: 1. neither lizard supplants the other; 2. displaying and moving toward, one flees; 3. lunging, one flees; and 4. jaw-locking, one flees.

The index well represents the level of intensity of aggression in an encounter (Table 3). Even within particular categories, encounters that qualitatively appeared to be more intense scored higher on the index of aggression. The one discrepancy involves several of the higher scoring encounters in the first category which scored higher than several of the lower scores in the second category. In the former encounters, the dominant lizard was fairly aggressive, adopting the poised position, but then subsiding without forcing the other lizard to flee. In the latter encounters, on the other hand, the subordinate lizard fled immediately after the dominant one jumped down from a perch toward it. These encounters probably would have scored appreciably higher if the subordinate lizard had not so promptly fled; the points awarded for forcing the other lizard to flee were not sufficient to compensate for those lost from the abrupt termination of the encounter. Notwithstanding this one shortcoming, the index appears to satisfactorily evaluate levels of intensity in aggressive encounters.

A second confirmation, with four exceptions, of the index's accuracy comes from comparison of the scores of the lizards judged dominant by their behavior, level of activity, and posture with the scores of those judged subordinate. In no case did the subordinate lizard achieve a higher score than the dominant lizard, while in four instances both lizards received the same score.

DISCUSSION

The male aggressive behavior of *A. marcanoi* appears very similar to that of most other *Anolis* studied, both overall and in particular

Table 3. Results of encounters between male *Anolis marcanoi*.

Encounter Outcome	Lizards Paired (I.D. Number, Higher Scoring Lizard First)	Dominant Lizard Score/Subordinate Lizard Score	Total Score
neither flees	9–18	0/0	0
	4–12	1/1	2
	5–9	5/1	6
	12–2	6/1	7
	14–16	8/3	11
	2–13	6/6	12
	1–7	8/8	16
	12–6	18/11	29
	14–3	18/11	29
	1–10	22/15	37
	19–5	23/14	37
displaying, one flees	3–9	15/6	21
	1–5	21/4	25
	3–9	26/6	32
	2–16	23/11	34
	13–17	23/12	35
	13–7	29/14	43
	5–4	32/18	50
lunging, one flees	11–7	35/17	52
	3–5	39/14	53
	14–7	39/15	54
	7–13	33/31	64
	13–12	36/28	64
jaw-locking, one flees	16–18	38/30	68
	19–15	41/29	70
	9–2	47/26	73

detail. The progressive nature of increasingly aggressive behavior has long been noted (Greenberg and Noble, 1944; Carpenter, 1967; Gorman, 1968; Jenssen, 1977, 1978; Hover and Jenssen, 1976; Ortiz and Jenssen, 1982). As in the study of five Puerto Rican *Anolis* by Ortiz and Jenssen, the behaviors and modifiers observed generally appeared in a progressive fashion, with some characteristically appearing early in encounters and others appearing progressively later as intensity increased. In most cases there was a clear linear path from one stage to another, though with one major exception, moving forward, which often preceded snout pointing. As noted above,

the ordering of some behaviors and display modifiers depended on distance separating the lizards. At a given distance, behaviors and modifiers generally did not appear prematurely, though many earlier behaviors and modifiers recurred at higher levels of intensity. A comparison of the index of aggression derived for *A. marcanoi* with that derived by Ortiz and Jenssen for Puerto Rican *Anolis* shows great similarity, though the latter is more detailed than the index presented here.

Particular behaviors also resemble those reported for related species. Stamps and Barlow (1973) reported several stages in the dewlap display of *A. aeneus*: fan, fanbob, bob, and jerkbob. Not only wereall four stages observed in *A. marcanoi,* but they appeared, very approximately, in equal proportions to those of *A. aeneus*. Crest erection, assumption of the faceoff position, lunging, and jawlocking have been observed in a number of species. Maximizing apparent size by body configuration and orientation is also prevalent among *Anolis* (Jenssen, 1977) and iguanids in general (Carpenter, 1967).

However, there are some differences in the behavior of *A. marcanoi* as well. Pointing with the snout has been reported for only one other species, *A. carolinensis* (and then only at very close range [Cooper, 1977]). *Anolis carolinensis* is also the only species reported to exhibit a well-defined postorbital dark spot. Behaviors noted occasionally in *A. marcanoi*, such as open mouth threats and mouthsmacking, are of greater importance in other species such as *A. opalinus* (Jenssen, 1979a) and *A. aeneus* (Stamps and Barlow, 1973), while actions never observed in *A. marcanoi*, such as tongue protrusion and foreleg lifting, have been observed in many other species (e.g., Rand, 1967; Jenssen, 1979a; Jenssen and Rothblum, 1977; Ortiz and Jenssen, 1982). It appears that as well as having its own stereotyped display-action patterns, each species of *Anolis* has its own behavioral repertoire, sharing some behaviors with other species while possessing a few unique behaviors of its own.

With regard to *A. cybotes*, two related questions merit addressing. Why is the aggressive behavior of *A. cybotes* so much simpler than that of *A. marcanoi*, and, indeed, of all *Anolis* examined? And why is there such little order in the appearance of aggressive behaviors, unlike the highly ordered and progresive pathways of increasing aggression in *A. marcanoi* and other *Anolis*?

Before these questions can be answered, several points of caution must be raised. First, it is possible that the experimental arena was not large enough to elicit the full range and ordering of natural aggressive behavior. Much larger experimental arenas have been used by other investigators (e.g., Jenssen, 1970, 1975; Jenssen and Hover, 1976; Stamps and Barlow, 1973), which was not possible in this case. If this is true, however, it is curious that the same problem did not occur in *A. marcanoi*, which is so similar to *A. cybotes*. Second, the lizards had been in captivity for more than ten months when the last of these experiments were performed. Though most appeared to be in reasonably good health, the long stretch of captive care may have taken its toll on their behavior. The lizards did, however, react quickly and in seemingly normal ways during the encounters; there was just no pattern from lizard-to-lizard or encounter-to-encounter. Third, the encounters involving *A. cybotes* were staged during the winter, a refractory period for males of the species in which their aggressive behavior is diminished in the wild (Jenssen, personal communication). Several *A. marcanoi* tested during the winter (which presumably is the refractory period for this species as well), after the same length of time in captivity, exhibited typical behavior.

Jenssen (1983) argues that the single stereotyped head-bobbing display pattern of *A. cybotes* is a primitive trait with respect to all *Anolis*. The rest of *A. cybotes*' aggressive behavior—dewlap displays, display modifiers, and advancing behavior—are also simpler and less ritualized than that of its sibling, *A. marcanoi*. That this simplicity could not be derived from the more complex behavior of *A. marcanoi*, however, is not clear.

Even if these behaviors are retained primitive ones, the ultimate question, why they have not been expanded and elaborated as in other species, still needs an answer. Jenssen (1983, personal communication) suggests that the determinants of social spacing in *A. cybotes*—a large lizard with large territories, few neighbors, low turnover, and low density—would mitigate against many territorial challenges. Lizards would know their neighbors and rarely challenge them. Intrusion would thus be a matter to be seriously dealt with because interlopers are likely to be lizards without a territory seeking to displace a resident, and because, due to low turnover, available territories would be hard to come by. Consequently, an

intrusion would rapidly result in a fight and elaborate communicatory rituals would be unnecessary. This hypothesis can explain the simplified aggressive behavior of *A. cybotes* compared to that of *A. distichus* (with which it was contrasted by Jenssen), but why such radical differences with its sibling species, *A. marcanoi*, and other truck-ground ecomorphs (*sensu* Williams, 1972), such as *A. cristatellus, A. cooki, A. gundlachi* (Ortiz and Jenssen, 1982), and *A. lineatopus* (Rand, 1967)? All that can be said is that nothing is known about the spacing and turnover of *A. marcanoi* populations, so direct comparisons with its sibling species cannot be drawn.

One important point can be made about the lack of distinct submissive behavior in *A. cybotes*. In *A. marcanoi*, submissive behavior appeared to have a pacifying effect on the dominant lizard. Only rarely and to a limited extent did a dominant lizard continue to act aggressively toward a clearly submissive opponent. By contrast, submissive behavior elicited no such complacency in *A. cybotes*. Most incidents of biting occurred upon lizards that were not displaying high levels of aggression. Consequently, submissive behavior did not seem to gain any advantage to the lizard displaying it. Rather, perhaps the best defense if escape is impossible is to put up an aggressive front, threatening retaliation in case of attack.

Whether these findings and speculations relate to natural behavior needs to be verified in the field. Studies are needed on the social structure and spacing of populations of both *A. marcanoi* and *A. cybotes* in nature. Futhermore, it is important to find out whether *A. cybotes* does, indeed, need a much greater space between individuals than *A. marcanoi* for naturally progressive behavior to appear.

Other than expanding the general pool of knowledge of *Anolis* behavior, the data here reported hopefully will be of value in investigating the ecological and behavioral interactions of these sibling species. Knowledge of the intraspecific behavior of males of both species will serve as a control with which to compare the results of experiments investigating interspecific male aggressive behavior and the mechanisms of species recognition.

ACKNOWLEDGMENTS

I am deeply indebted to Sibel Akyol, Pere Alberch, Ernest E. Williams, and, particularly, Greg Mayer for their continuous

encouragement, advice, and support. I am also deeply grateful to Sixto and Ivon Inchaustegui for their assistance when I was in the Dominican Republic. Thanks also to Emily Gale, Carlos Garcia, Harry Greene, Paul Hertz, Thomas Jenssen, James Knight, Jose Rosado, the members of the Herpetology Department, Museum of Comparative Zoology, and the staff of the Biological Laboratories, Harvard University, for their help, and to Crimson Camera for the loan of a video camera. Laszlo Meszoly and Gene Christman kindly drew the illustrations.

LITERATURE CITED

CARPENTER, C. 1962. Patterns of behavior in two Oklahoma lizards. Amer. Mid. Nat., **67**: 32–51.

———. 1965. Display of the Cocos Island anole. Herpetologica, **21**: 256–260.

———. 1967. Aggression and social structure in iguanid lizards, pp. 87–105. *In* W. W. Milstead (ed.), *Lizard Ecology: A Symposium*. Columbia, Mo., University of Missouri Press, ix + 300 pp.

———. 1978. Ritualistic social behaviors in lizards, pp. 253–267. *In* N. Greenberg and P. D. MacLean (eds.) *Behavior and Neurology of Lizards: An Interdisciplinary Colloquium*. Rockville, Md., NIMH, vii + 352 pp.

COOPER, W. E. 1977. Information analysis of agonistic behavioral sequences in male iguanid lizards, *Anolis carolinensis*. Copeia, **1977**: 721–735.

ECHELLE, A. A., A. F. ECHELLE, AND H. S. FITCH. 1971. A comparative analysis of aggressive display in nine species of Costa Rican *Anolis*. Herpetologica, **27**: 271–288.

GORMAN, G. C. 1968. The relationships of *Anolis* of the *roquet* species group (Sauria: Iguanidae)—III. Comparative study of display behavior. Breviora Mus. Comp. Zool., No. 284, pp. 1–31.

GREENBERG, B., AND G. K. NOBLE. 1944. Social behavior of the American chameleon (*Anolis carolinensis*). Physiol. Zool. **17**: 392–439.

GREENBERG, N. 1977. A neuroethological study of display behavior in the lizard *Anolis carolinensis*. Amer. Zool., **17**: 191–201.

HERTZ, P.E. 1980. Comparative physiological ecology of the sibling species *Anolis cybotes* and *A. marcanoi*. J. Herp., **14**: 92–95.

HOVER, E. L., AND T. A. JENSSEN. 1976. Descriptive analysis and social correlates of agonistic displays of *Anolis limifrons*. Behavior, **58**: 173–191.

JENSSEN, T. A. 1970. The ethoecology of *Anolis nebulosus* (Sauria, Iguanidae). J. Herp., **4**: 1–38.

———. 1975. Display repertoire of a male *Phenacosaurus heterodermus* (Sauria: Iguanidae). Herpetologica, **31**: 48–55.

———. 1977. Evolution of anoline lizard display behavior. Amer. Zool., **17**: 203–215.

———. 1978. Display diversity of anoline lizards and problems of interpretation, pp. 269–285. *In* N. Greenberg and P. D. MacLean (eds.), Behavior and Neurol-

ogy of Lizards: An Interdisciplinary Colloquium. Rockville, Md., NIMH, vi + 352 pp.

_____. 1979a. Display modifiers of *Anolis opalinus*. Herpetologica, **35**: 21–30.

_____. 1979b. Display behavior of male *Anolis opalinus* (Sauria, Iguanidae): A case of weak display stereotypy. Anim. Behav., **27** 173–184.

_____. 1983. Display behavior of two Haitian lizards, *Anolis cybotes* and *Anolis distichus*, 552 569. *In* A. G. J. Rhodin and K. Miyata (eds.), *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams*. Cambridge, Mus. Comp. Zool., x + 725 pp.

Jenssen, T. A., and E. L. Hover. 1976. Display analysis of the signature display of *Anolis limifrons*. Behavior, **57**: 227–240.

Jenssen, T. A., and L. Rothblum. 1977. Display repertoire analysis of *Anolis townsendi* (Sauria, Iguanidae). Copeia, **1977**: 103–109.

Mayr, E. 1942. *Systematics and the Origin of Species*. New York, Columbia University Press, x + 334 pp.

Ortiz, P. R., and T. A. Jenssen. 1982. Interspecific aggression bewteen lizard competitors, *Anolis cooki* and *Anolis cristatellus*. Z. Tierpsychol., **60**: 227–238.

Pace, A. E. 1974. Systematic and biological studies of the leopard frogs (*Rana pipiens* complex) of the United States. Miscellaneous Publications of the Museum of Zoology, Univ. of Michigan, **148**: 1–140.

Rand, A. S. 1967. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. Proc. U.S. Nat. Mus., **122**: 1–79.

Schoener, T. W. 1977. Competition and the niche, pp. 35–136. *In* C. Gans and D. W. Tinkle (eds.) Biology of the Reptilia, Vol. 7. London, Academic Press, viii + 720 pp.

Schwartz, A. 1974. An analysis of variation in the Hispaniolan giant anole *Anolis ricordii* Dumeril and Bibron. Bull. Mus. of Comp. Zool., **146**: 89–146.

Stamps, J. A., and G. W. Barlow. 1973. Variation and stereotypy in the displays of *Anolis aeneus*. Behavior, **47**: 67–94.

Webster, T. P. 1975. An electrophoretic comparison of the Hispaniolan lizards *Anolis cybotes* and *A. marcanoi*. Breviora Mus. Comp. Zool., No. 431, pp. 1–8.

Williams, E. E. 1965. The species of Hispaniolan green anoles (Sauria: Iguanidae). Breviora Mus. Comp. Zool., No. 227, pp. 1–16.

_____. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. Evol. Biol., **6**: 47–89.

_____. 1975. *Anolis marcanoi* new species: sibling to *Anolis cybotes*: description and field evidence. Breviora Mus. Comp. Zool., No. 430, pp. 1–9.

B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 29 AUGUST 1986 NUMBER 485

THE ANATOMY AND RELATIONSHIPS OF *STEREOPHALLODON* AND *BALDWINONUS* (REPTILIA, PELYCOSAURIA)

DONALD BRINKMAN[1] AND DAVID A. EBERTH[2]

ABSTRACT. As representatives of pelycosaurs from the earliest terrestrial deposits of the Texas and New Mexico Permo-Pennsylvanian sequence, *Stereophallodon* and *Baldwinonus* are important in our understanding of pelycosaur evolution. However, their variable placement in the phylogenetic schemes of Romer and Price (1940), Langston (1965), and Reisz (1980) has underscored the fact that their morphology is poorly known and that their relationships are openly questioned. Reanalysis of previously described specimens and heretofore undescribed specimens has allowed for a reevaluation of both the morphology of *Stereophallodon* and *Baldwinonus* and the phylogenetic relationships of these taxa with other pelycosaurs.

Stereophallodon is interpreted as the sister-taxon of *Ophiacodon* on the basis of five derived features: the shape of the cultriform process, the ventrally directed basipterygoid process, the anteroposteriorly oriented basipterygoid articular surfaces, the presence of a ridge that is triangular in cross section extending dorsally from the caniniform-tooth buttress, and the presence of a notch on the postero-medial edge of the quadrate. *Stereophallodon* is primitive with respect to *Ophiacodon* in retaining the following characters: dorsal vertebrae that have flattened ventral surfaces and subparallel sides, a femur with an adductor crest running along the mid-ventral surface of the bone, and a long neck on the astragalus. Apomorphic features of *Stereophallodon* are the presence of two greatly enlarged caniniform teeth supported by a caniniform-tooth buttress and the triangular cross section of the proximal end of the fibula.

[1]Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta, Canada, T0J 0Y0

[2]Tyrrell Museum of Palaeontology, Box 7500, Drumheller, Alberta, Canada, T0J 0Y0

Baldwinonus is represented by the weathered remains of a single individual from New Mexico. It is considered related to *Stereophallodon* on the basis of shared derived features of the maxilla.

INTRODUCTION

In a previous paper (Brinkman and Eberth, 1983), the interrelationships of a number of genera of pelycosaurs were considered. The genera included representatives of most of the families recognized by Romer and Price (1940), and thus the analysis served as a test of their long accepted phylogeny. The relationships of the Ophiacodontidae, Edaphosauridae, and Sphenacodontidae that they proposed were supported by this analysis, but the relationships of the Varanopseidae and the Caseidae were not. Rather than considering *Varanops* and *Aerosaurus* as primitive sphenacodonts and *Casea* as a primitive edaphosaurian, it was concluded that these genera are members of a single clade that is primitive in a number of features with respect to the clade that includes *Dimetrodon, Edaphosaurus,* and *Ophiacodon.*

Brinkman and Eberth restricted their analysis to better preserved taxa in order to establish "...a framework in which detailed taxonomic and morphological revisions of individual genera and families can be interpreted." (Brinkman and Eberth, 1983: 3). Since that review, two problematic taxa, *Stereophallodon* and *Baldwinonus,* have been studied by the authors and their relationships with other pelycosaurs have been reevaluated. In this paper, we describe the morphology of these two taxa and present our phylogenetic conclusions.

Stereophallodon was first described by Romer (1937: 90) and was characterized by the presence of "ophiacodont" vertebrae and two greatly enlarged caniniform teeth. In a later description (Romer and Price, 1940), it was stated that *Stereophallodon* differed from *Ophiacodon* in the presence of two large caniniform teeth, the greater development of the prefrontal pocket, abrupt decrease in length of the postcaniniform teeth, and in showing a tendency towards a greater ventral flattening of the centra. In the same paper, Romer and Price (1940) named a new pelycosaur, *Baldwinonus trux,* and described it as having ophiacodont-like quadrate, vertebral and tooth morphology, but sharing with *Stereophallodon* the specialized characters of enlarged caniniform teeth, close-set

zygapophyses and flattened ventral centra. Noting similar carnivorous specializations in the diminutive *Eothyris,* considered by Romer and Price to be an especially primitive ophiacodont, and *Stereorhachis,* a pelycosaur from Autun, France, with *Ophiacodon*-like postcrania, Romer and Price erected the taxon Eothyrididae for the inclusion of *Eothyris, Baldwinonus, Stereophallodon,* and *Stereorhachis* and characterized the family as follows:

> Ophiacodont pelycosaurs, primitive in most known regards but paralleling the higher sphenacodonts in the development of much enlarged canines and showing a tendency towards elongation of the vertebral column (Romer and Price, 1940: 246–247).

The occurrence of *Stereophallodon* in the earliest terrestrial deposits of the Texas Permo-Pennsylvanian sequence (Pueblo Formation) led Romer and Price to suggest that the eothyridids represented an early radiation of carnivorous pelycosaurs that, ecologically, were supplanted by sphenacodonts and were, in themselves, a phyletic dead end. Contrary to this opinion, Watson (1954, 1957) suspected a close phylogenetic relationship between *Eothyris* and the caseids, *Casea* and *Cotylorhynchus.* According to Romer and Price (1940) the caseids were derived from an obscure group, the Nitosauridae, the taxa of which appear to be based on fragmentary remains of questionable association (Reisz, 1980). Watson's insight gained more firm support following Vaughn's 1958 description of *Colobomycter pholeter,* a small pelycosaur from the Fort Sill fissure fills of Oklahoma that displays strong affinities to both *Eothyris* (short face, anteroposteriorly thickened postorbital bar, large supratemporal, large parietal foramen, large naris and similar maxillary dentition) and caseids in general (rugose skull, short face, large naris, large supratemporal, large parietal foramen and the presence of an infraorbital foramen). Langston (1965) described a new pelycosaur from the Cutler Formation of north-central New Mexico (*Oedaleops*) that likewise showed a number of features shared in common by the eothyridids *Eothyris* and *Colobomycter* and the caseids. His reevaluation of the eothyridid relationships within the Pelycosauria led him to conclude (as had Vaughn) that the Eothyrididae (including *Stereophallodon, Stereo-*

rhachis, Baldwinonus, Eothyris, Oedaleops, Colobomycter, as well as three genera no longer accepted as members of that family, the very poorly known *Delorhynchus, Bayloria* and *Tetraceratops*) were antecedent to the caseids and that, in contradiction to Romer and Price, the nitosaurids represented a phyletic dead end group of ophiacodonts convergent with caseids in only a few characters of proportion. Most recently, Reisz (1980), in a cladistic analysis of pelycosaur families, concluded that the relationship between eothyridids (*Eothyris* and *Oedaleops*) and caseids was well founded, citing the shared derived characters of an overhanging rostrum, an elongate narial opening, and a maxillary contribution to the ventral border of the orbit.

While the *Eothyris, Oedaleops, Colobomycter*/Caseidae relationship appears now to be well established, the position of *Stereophallodon, Stereorhachis,* and *Baldwinonus* are less certain. Langston (1965) chose to retain these taxa within the Eothyrididae although he cited the enlarged caniniform teeth as the only reason for doing so and remained uncertain of the validity of the grouping. Reisz went one step further and removed *Stereorhachis* and *Stereophallodon* from the Eothyrididae and placed them in the Ophiacodontidae, (1980: 566, 568). He questioned the reality of *Baldwinonus,* identifying the maxilla and neural spines of the type specimen as a sphenacodont and the vertebrae as pertaining to an ophiacodont. In our previous paper, (Brinkman and Eberth, 1983) we have questioned Reisz's phylogeny and have proposed a different arrangement. For this reason and the fact that the relationships of *Baldwinonus, Stereophallodon,* and *Stereorhachis,* and the validity of *Baldwinonus* remain uncertain, and because a number of new specimens of *Stereophallodon* have become available, we have undertaken a review of the specimens of these taxa available to us for examination. *Stereorhachis,* known from the Stephanian near Autun, France, was not available for study and must unfortunately remain excluded from the following analysis. In considering the position of *Baldwinonus* and *Stereophallodon* the phylogenetic conclusions of our earlier study were tested and our understanding of the morphological diversity present in pelycosaurs has been increased.

MATERIALS AND METHODS

The methods used in interpreting polarities of the character-states are those outlined by Brinkman and Eberth (1983: 3). In that analysis, the polarity of character-states was interpreted using outgroup comparison. All other reptiles were considered the closest sister-group to the pelycosaurs; diadectomorphs were considered the closest sister-group to the pelycosaurs and all other reptiles; and anthracosaur amphibians were considered the sister-group of the clade composed of the foregoing taxa. This framework is used as a basis for interpreting polarities in this study as well.

The following specimens were examined during the course of this work:

AMNH 4780: (type and only known specimen of *Baldwinonus trux*) fragmentary remains of a single individual including maxilla, quadrate, twelve partial vertebrae, and partial ribs;

MCZ 1535: (type of *Stereophallodon ciscoensis*) fragmentary remains of a single individual including the premaxilla, maxilla, quadrate, articular, left half of occiput, and five centra;

MCZ 1944: fragmentary remains of a single large individual identified as *Stereophallodon* on the basis of the maxilla and articular;

MCZ 6618: fragmentary remains of a single large individual, identified as *Stereophallodon* on the basis of the quadrate and articular;

AMNH 4768: associated vertebrae, sacral ribs and premaxilla of a single large individual, identified as *Stereophallodon* on the basis of the premaxilla and the similarity of the vertebrae with those preserved in MCZ 6618.

A number of isolated elements present in the collections from Prideaux Pocket, a bonebed in the Pueblo Formation, can be identified as belonging to *Stereophallodon.* These include: MCZ 6358, three premaxillae; MCZ 6354, five maxillary fragments; MCZ 6352, two prefrontals; MCZ 6353, one postfrontal; MCZ 6348, five

basioccipitals; MCZ 6349, three basi-parasphenoids; MCZ 6350, four quadrates; MCZ 6359, eight dentary fragments; MCZ 6352, three articulars; MCZ 6371, one axis centrum; MCZ 6357, partial centrum of a cervical vertebra; MCZ 6355, twenty mid-dorsal centra; MCZ 6356, twenty-two centra from various positions along the vertebral column; MCZ 6768, three ilia; MCZ 7083, part of the distal end of a femur; MCZ 6766, proximal end of femur; MCZ 6765, two proximal ends of fibulae; and MCZ 6767, four proximal ends of tibiae.

The following acronyms are used in this paper; AMNH, American Museum of Natural History; MCZ, Museum of Comparative Zoology; UCMP, University of California, Berkeley, Museum of Paleontology.

DESCRIPTION

Stereophallodon

An almost complete premaxilla is preserved in AMNH 4768 (Fig. 1A–B). This has a posteriorly sloping dorsal ramus and a tooth bearing base. A foramen is present on the posterior surface of the premaxilla at the base of the dorsal ramus. Sockets for five teeth are present in the premaxilla. The diameter of the anterior two sockets is about twice that of the more posterior sockets. The premaxilla of *Stereophallodon* is like that of *Ophiacodon* (Fig. 1D) and different from that of the sphenacodontines (Fig. 1E) in the structure of the dorsal ramus. In *Stereophallodon* and *Ophiacodon* the posterior edge of the dorsal ramus meets the tooth-bearing base of the bone just above the maxillary suture. In the sphenacodontines, the posterior edge of the dorsal ramus meets the base of the premaxilla anterior to the maxillary suture.

The maxilla (Fig. 1C) is represented by a number of specimens which show a caniniform-tooth buttress and adjacent areas. The sutural surface for the palatine extends forward onto the buttress to a point above the exposed posterior edge of the second caniniform tooth. The maxilla is broken at the dorsal apex of the buttress. The horizontal cross section at this point shows that a rodlike brace extended dorsad from the buttress along the inner surface of the maxilla as in *Ophiacodon*. In the sphenacodontines no such ridge is present; the caniniform-tooth buttress is a broad, gently contoured wedge of bone that merges smoothly and evenly with the medial

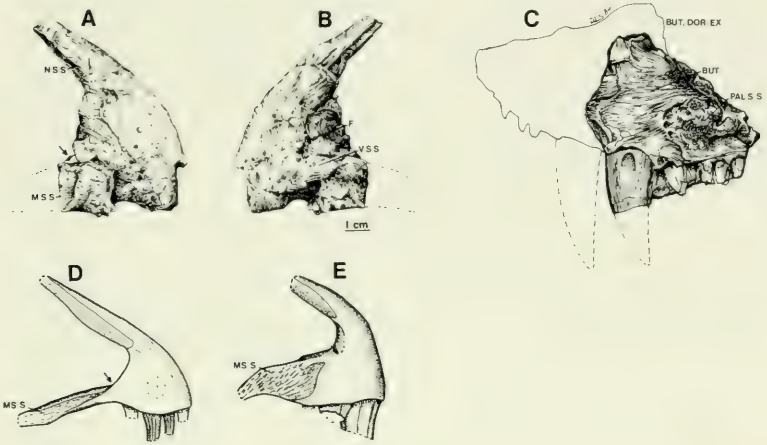


Figure 1. The right premaxilla of *Stereophallodon* in A) lateral and B) medial views; C) the right maxilla of *Stereophallodon* in medial view; D) the right premaxilla of *Ophiacodon* in lateral view, and E) the right premaxilla of *Sphenacodon* in lateral view. Arrows on the premaxillae indicate the posteroventral edge of the dorsal ramus of the premaxilla. *Stereophallodon* premaxilla drawing based on AMNH 4768, reconstructed portion based on the articular surface for the premaxilla preserved on the maxilla in MCZ 1944; shaded portion of the maxilla drawing based on MCZ 1535, with the outline drawn on the basis of MCZ 1944; *Ophiacodon* drawing based on UCMP 40035; and *Sphenacodon* drawing based on UCMP 83047.

Abbreviations: BUT, caniniform-tooth buttress; BUT, DOR, EX, dorsal extension of the caniniform-tooth buttress; F, foramen; M S S, maxillary sutural surface; N S S, nasal sutural surface; PAL S S, palatine sutural surface; V S S, vomer sutural surface.

surface of the maxilla. Moreover, a precaniniform-tooth step is not present in *Stereophallodon*. Rather, the ventral edge of the maxilla slopes gently dorsally and bears well-developed precaniniform teeth.

Two large caniniform teeth are present on the maxilla, each having a basal diameter of about three times that of any of the more posterior teeth. At least three teeth are present anterior to the caniniform teeth. The postcaniniform teeth, as described by Romer and Price (1940), are extremly short, measuring about one sixth the length of the caniniform teeth, and are more broadly exposed on the internal surface of the maxilla than on the external surface.

Fragments of the dermal skull elements present in the type specimen include the prefrontal, postfrontal, and frontal. Isolated

prefrontals are present in the Prideaux Pocket locality. These elements show that the frontal of *Stereophallodon* is like that of *Ophiacodon* in having a small lateral lappet. The prefrontal has a lateral pocket anterior to the orbit, although this does not seem significantly larger than a similar pocket seen in the prefrontal of larger specimens of *Ophiacodon.*

Pterygoids are preserved in MCZ 1944 (Fig. 2A). The right and left pterygoids are preserved together in a single block with the transverse flange of the right pterygoid visible in dorsal view and the quadrate ramus of the left pterygoid visible in medial view. The tip of the transverse flange of the right pterygoid is preserved separately (Fig. 2C). As in *Ophiacodon* (Fig. 2B), a tympanic flange extends

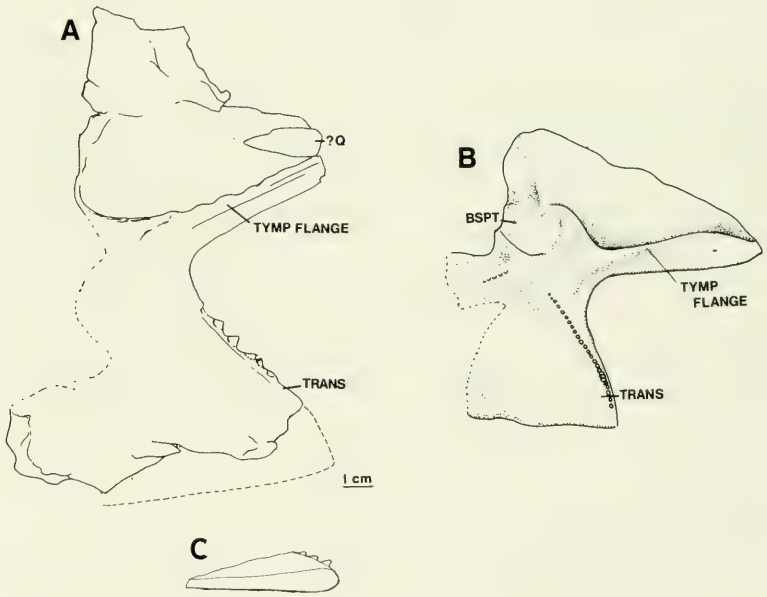


Figure 2. The right pterygoid of A) *Stereophallodon* and B) *Ophiacodon* in medial view and C) lateral view of the transverse flange of the pterygoid of *Stereophallodon.* Drawing of *Stereophallodon* a composite based on right and left pterygoid preserved in MCZ 1944. *Ophiacodon* drawn from MCZ specimen.

Abbreviations: BSPT, basipterygoid articular surface; TRANS, transverse flange of the pterygoid; TYMP FLANGE, tympanic flange; ?Q, ?Quadrate.

medially from the ventral edge of the quadrate ramus of the pterygoid. The transverse flange of the pterygoid is like that of *Ophiacodon* in that its lateral edge is thinner relative to its height than that of *Dimetrodon.* This difference is consistent in both large and small specimens of *Dimetrodon* and *Ophiacodon* and thus is independent of size. As in *Ophiacodon,* a single row of many small teeth is present on the ventral edge of the transverse flange. Five teeth are preserved, and more were probably present on the missing portion of the transverse process (dashed area, Fig. 2A).

Quadrates are present in MCZ 1535 (Fig. 3A–C) and MCZ 6618. Four isolated quadrates are present in the material from Prideaux Pocket. The articular surface is differentiated into two condyles with a saddle-shaped surface extending between them. The lateral condyle has articular surface extending from its medial to its lateral surface. The medial condyle has articular surface developed only on its lateral and ventral surfaces. A stapedial pit is present on the medial edge of the bone just above the medial condyle. This is a shallow depression containing a round tuberosity. In posterior view the dorsal edge of the quadrate is notched. This notch is similar in position to the shelf on the posteromedial surface of the quadrate as in *Ophiacodon* and is considered a less well-developed stage of the same character. The shape of the articular surface in the two genera is different in that the lateral condyle is broader mediolaterally in *Stereophallodon* than in *Ophiacodon.*

The left half of the occiput is preserved in MCZ 1535 (Fig. 4). Although not visible in this view, the fused supraoccipital and

Figure 3. The right quadrate of *Stereophallodon* in A) posterior, B) medial, and C) articular views. Drawing based on MCZ 1535.

Abbreviations: LAT COND, lateral condyle; MED COND, medial condyle; NOTCH, notch in dorsal edge of quadrate; S, stapedial pit.

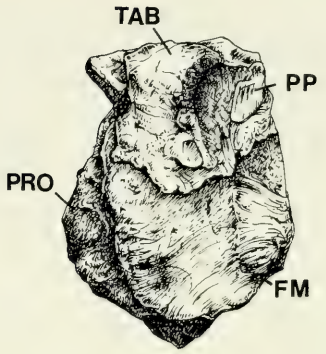


Figure 4. Left half of the occiput of *Stereophallodon*, posterior view. Drawing based on MCZ 1535.

Abbreviations: F M, dorsal edge of foramen magnum; PP, postparietal; PRO, prootic; TAB, tabular.

prootic end laterally in an oval area of unfinished bone as in *Ophiacodon.* Romer and Price (1940) identified a piece of bone on the lateral corner of the supraoccipital as a displaced postparietal. However, a separate element is present medial to this in a position normally occupied by the postparietal in all other pelycosaurs and is thus more reasonably interpreted as that element. The more lateral bone is therefore interpreted as a fragment of the tabular.

A nearly complete basi-parasphenoid is present in MCZ 1944 (Fig. 5), and, based on this specimen, a number of fragmentary basi-parasphenoids can be identified among the Prideaux Pocket material. As in *Ophiacodon,* the basipterygoid processes are directed ventrally and the long axis of their articular surfaces are oriented anteroposteriorly. The cultriform process is like that of *Ophiacodon* in being nearly as wide as it is high. This is unlike the condition in *Dimetrodon* and *Edaphosaurus* where the cultriform process is more bladelike in cross section. The basi-parasphenoid wings are broadly separated. A small shelf covers the anterior portion of the groove between the wings.

Five isolated basioccipitals from Prideaux Pocket can be referred to *Stereophallodon* (Fig. 6) on the basis of their large size. No other pelycosaur from that locality is as large. These are like the basioccipitals of *Ophiacodon* in that the occipital condyles are

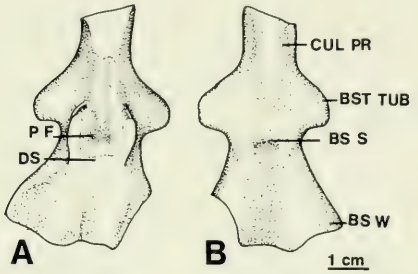


Figure 5. Basi-parasphenoid of *Stereophallodon* in A) dorsal and B) ventral views. Drawing based on MCZ 1944.

Abbreviations: BS S. basisphenoid shelf; BST TUB, basipterygoid tubercula; BS W, basi-parasphenoid wings; CUL PR, cultriform process; D S, dorsum sella; P F, pituitary fossa.

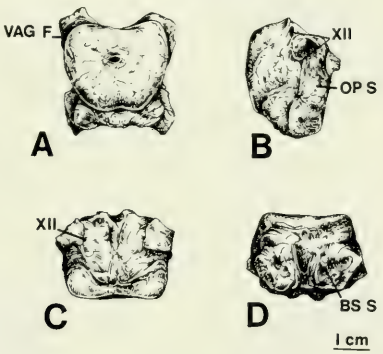


Figure 6. Basioccipital of *Stereophallodon* in A) posterior, B) right lateral, C) dorsal, and D) ventral view. Drawing based on MCZ 6348.

Abbreviations: BS S, basi-parasphenoid sutural surface; OP S, opisthotic sutural surface; VAG F, medial edge of vagus foramen; XII, foramen for twelfth cranial nerve.

flattened inferiorly. Also, in both genera, the ventral surface is marked by a series of ridges and grooves between the basioccipital tubercula. In *Dimetrodon* and *Edaphosaurus,* no ridges are present on the ventral surface of the basioccipital between the basioccipital tubercula.

Articulars are present in MCZ 1535 (Fig. 7), MCZ 1944, and MCZ 6618. Three articulars are known from the Prideaux Pocket locality. The most complete of these is MCZ 6618, in which the angular and prearticular remain in sutural contact with the articular. The shape of the cotyles correspond to the condyles of the quadrate: the lateral cotyle is a cup-shaped depression, and the medial cotyle faces medially. No retroarticular process is present on the articular. Instead, a ridge extends from the ventral edge of the angular to the posterior tip of the articular. A distinct process for

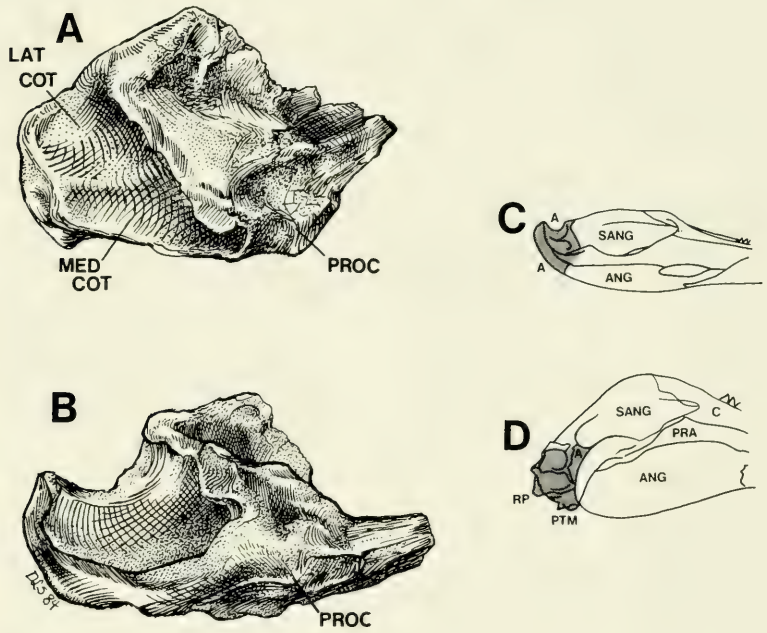


Figure 7. Articular of *Stereophallodon* in A) dorsal, and B) medial views, and the posterior end of the jaw of C) *Ophiacodon* and D) *Dimetrodon*. *Stereophallodon* drawing based on MCZ 1535, *Ophiacodon* and *Dimetrodon* from Romer and Price (1940).

Abbreviations: A, articular; ANG, angular; C, coronoid; LAT COT, lateral cotyle; MED COT, medial cotyle; PRA, prearticular; PROC, medial process on angular; PTM, pterygoid process of articular; RP, retroarticular process; SANG, surangular.

muscle attachment is present on the angular just anterior to the articular. As in *Ophiacodon* and *Varanops,* this is a medially directed process that is triangular in dorsal view. In *Dimetrodon* and *Edaphosaurus* the process is formed by the articular and it extends ventromediad. The articular has a ridge on its ventral surface that marks the limit of contact with the angular. As in *Ophiacodon, Edaphosaurus,* and *Dimetrodon,* the angular extends below the adductor fossa as a ventrally extended platelike element.

The anterior end of the dentary is preserved in specimen MCZ 1944, and a number of dentary fragments are known from Prideaux Pocket. In contrast to the slender dentary of *Ophiacodon,* the dentary of *Stereophallodon* is robust and deep. The anterior three teeth are enlarged, although they are smaller than the caniniform teeth of the maxilla. Behind these, the dentary narrows mediolaterally, presumably to allow the upper caniniform teeth to pass lateral to the dentary.

Twenty associated vertebrae are present in AMNH 4768. These include two sacral, four caudal, four lumbar, and ten dorsal vertebrae. Some of these are preserved in articulation. An atlas centrum and axis are present in MCZ 1944. The axis and four centra from the cervical or anterior dorsal region are present in MCZ 1535, and a number of isolated centra are known from Prideaux Pocket. An atlas intercentrum from this locality is referred to *Stereophallodon* on the basis of its large size. Thus most morphological areas along the vertebral column are represented, although the total number of presacral vertebrae and the number of vertebrae present in each area is unknown.

The atlas centrum is directly comparable to the fused atlas centrum and axis intercentrum of an adult *Ophiacodon* in outline, position of notochordal pits, and width of the ventral surface. Thus, although no sutures are visible, it is assumed that the axis intercentrum is fused to the atlas centrum in this specimen.

The axis is keeled. Anteriorly, a well-developed lip is present to receive the intercentrum (Fig. 8A). The transverse processes are short and slop ventrolaterally.

The four more posterior cervical and anterior dorsal centra preserved in MCZ 1535 show a transition from a keeled ventral surface on the cervical centra to a flattened ventral surface possessing a pair of widely separated ventral ridges on the anterior

Figure 8. A–J) vertebrae of *Stereophallodon.* A) axis, B) anterior cervical vertebra; C) mid-cervical vertebra; D) anterior dorsal vertebra; E) dorsal vertebra; F) lumbar vertebra; G) sacral vertebra in lateral and ventral views. H) dorsal vertebra in proximal view; I) lumbar vertebra; J) and sacral vertebra in distal views. K–N) cross sections of dorsal vertebrae of K) *Stereophallodon*; L) *Ophiacodon;* M) *Edaphosaurus;* and N) *Dimetrodon.* Drawings A–D based on MCZ 1535; E–I based on AMNH 4768; and K–N from Romer and Price (1940).

Abbreviations: CAP ART SURF, capitular articular surface; IC, intercentrum; KEEL, mid-ventral keel; LIP, anterior lip on axis; POST ZYG, postzygapophysis; PRE ZYG, prezygapophysis; RIB, lumbar rib in place; SAC RIB, sacral rib; TRANS PR, transverse process.

dorsal centra. The most anterior of the cervicals is broadly rounded in cross section; its ventral surface possesses a midline keel and two, more lateral, longitudinal ridges (Fig. 8B). The intercentrum is preserved in place. Without it, a well-developed lip would be present. A large articular surface for the head of the rib is present on each side of the centrum. This extends onto the intercentrum. The

second vertebra in this series (Fig. 8C) is approximately wedge-shaped in cross section, but has a pair of closely placed ridges ventrally rather than a single mid-ventral keel. The capitular articular surfaces are less well developed than in the more anterior vertebra. A lip to receive the intercentrum is not present. The following two vertebrae, the best of which is illustrated in Figure 8D, are more rectangular in cross section. The pair of ridges on the ventral surface of the centrum are widely separated (Fig. 8D). The articular surface for the capitular head of the rib is very small in comparison to the more anterior vertebrae.

Ten dorsal vertebrae are present in AMNH 4768. These are subrectangular in end view and in cross section (Fig. 8H). The ventral surfaces of each centrum is flattened and does not possess a keel (Fig. 8E). The ventral half of the lateral surfaces of the centra are subparallel to one another dorsoventrally. A small articular surface for the capitular head of the rib is located near the dorsal edge of each centrum. The transverse processes are short and are separated from the capitular articular surfaces by a small notch. The zygapophyses are set close to the midline and are strongly sloped. The neural spines are short, their height being about one and a half times the height of the centrum. The spines are expanded anteroposteriorly at their tips.

Four lumbar vertebrae are present in AMNH 4768 (Fig. 8F). These differ from the dorsal vertebrae in being wider and having a trefoil-shaped cross section. In end view (Fig. 8I) the centrum is round, rather than sub-rectangular as in the dorsal vertebrae. The articular surfaces for the ribs on the lumbars are larger than those on the dorsal vertebrae, and in some specimens ribs remain in place, fused to the centrum. The zygapophyses are more nearly horizontal than they are in the dorsal vertebrae. The neural spines are similar to those of the dorsal vertebrae in their proportions and structure.

The sacral vertebrae can be identified by the exaggeration in the size of the rib articular surfaces. The ventral half of the centrum is compressed mediolaterally, forming a rounded ventral ridge that extends between the ends of the centrum (Fig. 8G). The zygapophyses are similar to those of the dorsal vertebrae in being large, sub-horizontally oriented surfaces. The neural spine is narrower anteroposteriorly than in the more anterior vertebrae, and slopes posteriorly. The centrum is oval in end view (Fig. 8J).

The caudal vertebrae are round in cross section. The articular surfaces for the ribs are large, the capitular articular surfaces being slightly smaller than the tubercular surfaces. Both the proximal and distal edges of the centrum are deeply bevelled for the intercentra.

The anterior cervical vertebrae of *Stereophallodon* are like those of *Ophiacodon, Edaphosaurus,* and the sphenacodontines: the centra are keeled and the anterior end is strongly bevelled for the intercentrum. The dorsal vertebrae of *Stereophallodon* bear little resemblance to those of *Ophiacodon, Edaphosaurus,* or the sphenacodontines. In *Ophiacodon,* the mid-dorsal vertebrae are wedge-shaped in cross section (Fig. 8L) and the posterior dorsal vertebrae are circular in end view and in cross section. Vertebrae that are subrectangular in cross section like those of the dorsal vertebrae of *Stereophallodon* (Fig. 8K) are not present. The dorsal vertebrae of *Edaphosaurus* differ from those of *Stereophallodon* in that in cross section the centra are rounded rather than flattened ventrally (Fig. 8M). The sphenacodontines have dorsal vertebrae that are strongly keeled (Fig. 8N). The lumbar vertebrae of *Stereophallodon* are unlike those *Ophiacodon, Edaphosaurus,* or the sphenacodontines in having a centrum that is trefoil-shaped in cross section.

The proximal end of the ulna is present in MCZ 6618 (Fig. 9). The element is broad, medio-laterally flattened, and its posterior edge is strongly convex. The trochlear notch is shallow and has a distinct articular surface for the proximal end of the radius. The ulna of *Stereophallodon* is like that of *Ophiacodon* in being broad at the level of the trochlear notch. In *Edaphosaurus* and *Dimetrodon* the ulna is narrower in this area.

The acetabular region of the pelvis is present in MCZ 6618 (Fig. 10). Three partial ilia are present in the collection from the Prideaux Pocket. The ilium lacks an anterior process and has only a short posterior process. As in *Ophiacodon* and *Ruthiromia,* a shelf extends medially above the area of articulation with the sacral rib. This shelf is located at the dorsal edge of the iliac blade.

The distal end of the femur is present in MCZ 6618 (Fig. 11). As in primitive reptiles generally, the dorsal surface of the distal end of the femur has a well-developed intercondylar groove. The finished bone covering this groove extends around the distal end of the femur towards the fibula. The shaft of the femur is circular in cross section and the adductor crest is a low ridge extending along its

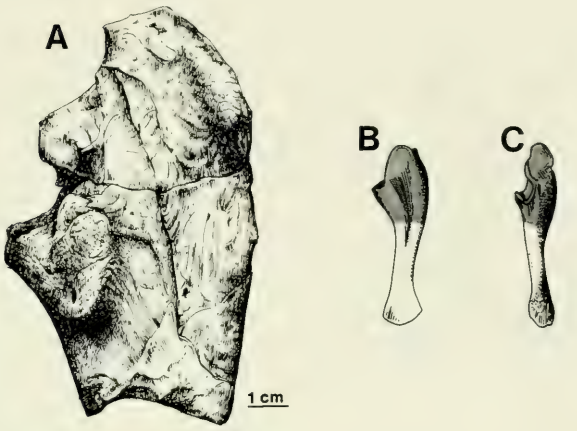


Figure 9. Proximal end of ulna of A) *Stereophallodon* and ulna of B) *Ophiacodon,* and C) *Dimetrodon.* Drawing of *Stereophallodon* based on MCZ 6618. Drawings of *Ophiacodon* and *Dimetrodon* from Romer and Price (1940).

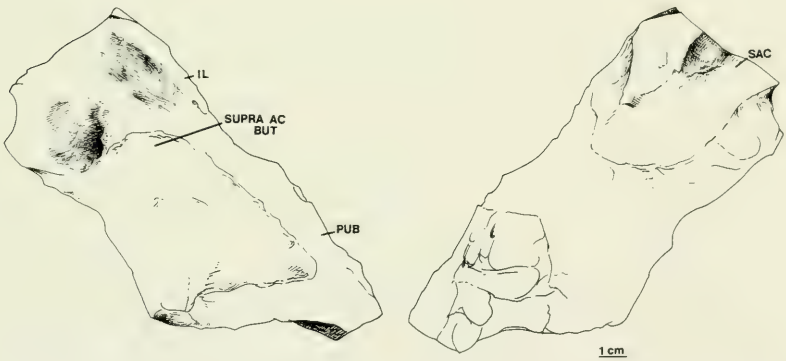


Figure 10. Partial pelvis of *Stereophallodon* in lateral and medial views. Drawing based on MCZ 6618.

Abbreviations: IL, ilium; PUB, pubis; SAC, articular surface for sacral rib; SUPRA AC BUT, supra-acetabular buttress.

mid-ventral surface. This is different from the condition in *Ophiacodon,* where the ridge is a sharp crest located along the fibulad edge

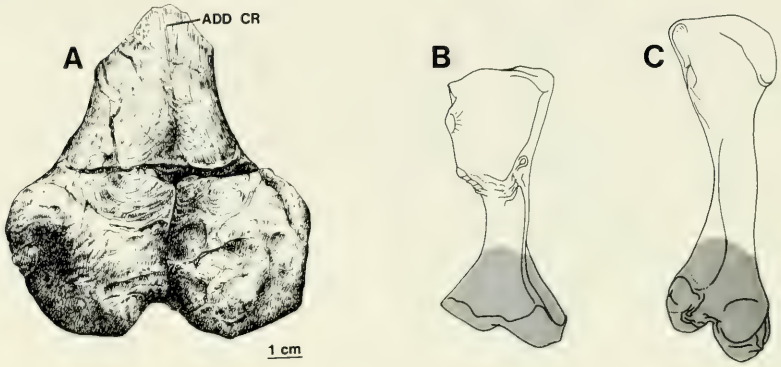


Figure 11. Right femur of A) *Stereophallodon*, B) *Ophiacodon* and C) *Dimetrodon*. *Stereophallodon* drawn from MCZ 6618. *Ophiacodon* and *Dimetrodon* from Romer and Price (1940).

Abbreviations: ADD CR, adductor crest.

of the bone. In *Ruthiromia, Casea,* and *Edaphosaurus,* the adductor crest is located in a mid-ventral position, but this is a sharp crest rather than a low rugosity, and gives the femur a tear-drop-shaped cross section.

The proximal end of the left tibia and the shaft and the distal end of the right tibia are preserved in MCZ 6618. Three proximal ends of tibiae are present in the material from Prideaux Pocket. This element (Fig. 12) is much more fully ossified than any tibia known in *Ophiacodon,* so detailed comparison is not possible with that genus. The element differs from the tibiae of *Dimetrodon* and *Edaphosaurus* in that the outline of the lateral condyle of the articular surface is circular, rather than oval in articular view. The shaft has well-developed ridges on both the medial and lateral surfaces. Well-developed ridges are present on the lateral edges of all other pelycosaur tibiae examined. A slight ridge is present on the internal edge of the tibia in *Ophiacodon,* although it is not as strongly developed. *Ruthiromia* is similar to *Stereophallodon* in having a well-developed ridge on the internal surface of the tibia.

The proximal and distal ends of a fibula are present in MCZ 6618. Two proximal ends of fibulae are present in the material from

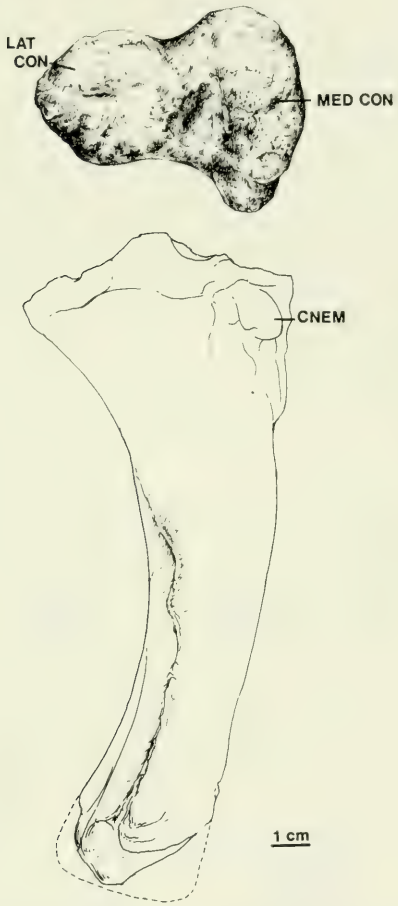


Figure 12. Left tibia of *Stereophallodon* in articular and anterior views. Anterior view is a composite drawing based on right and left elements present in MCZ 6618.

Abbreviations: CNEM, cnemial tuberosity; LAT CON, lateral condyle, MED CON, medial condyle.

Prideaux Pocket (Fig. 13). The proximal end of the fibula is triangular in proximal view, with the base of the triangle forming the articular surface for the femur. A muscle scar is present on the lateral tip of the triangle. The proximal end of the fibula is unlike

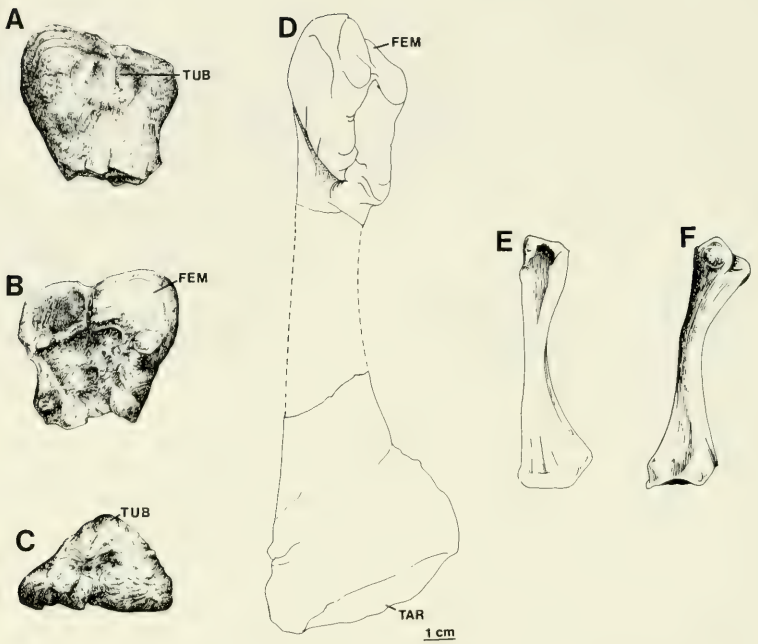


Figure 13. A–C) the proximal end of the right fibula of *Stereophallodon*, in A) lateral view, B) medial view, and C) proximal view; D) left fibula of *Stereophallodon*, actual length unknown; E) *Ophiacodon,* and F) *Dimetrodon. Stereophallodon* drawing based on MCZ 6618, *Ophiacodon* and *Dimetrodon* from Romer and Price (1940).

Abbreviations: FEM, articular surface for femur; TAR, articular surface for tarsus; TUB, tuber of uncertain function.

those of other pelycosaurs in its triangular shape. In *Ophiacodon, Dimetrodon,* and *Edaphosaurus* the proximal end of the fibula is rectangular in end view and has a proximo-distally oriented tuberosity on its lateral edge. The distal end of the fibula of *Stereophallodon* is wide and dorso-ventrally compressed. The astragalar and calcaneal articular surfaces are set at a low angle to each other and are differentiated by a slight narrowing of the distal end of the bone. *Ophiacodon, Edaphosaurus,* and *Ruthiromia* are like *Stereophallodon* in having broad distal ends of the fibulae. In sphenacodontines, the distal end of the fibula is narrower mediolaterally.

A nearly complete left astragalus and the distal half of the right astragalus are present in MCZ 6618 (Fig. 14). As in primitive reptiles generally, this element is L-shaped with a tibial articular surface located on the lateral branch of the L, and the dorsal branch contributes to the support of the fibula. A perforating notch is present on the lateral face of the astragalus. The proportions of the astragalus are like those of the element in *Edaphosaurus* in that the neck is elongate, constituting nearly half of the proximodistal length of the bone. This is unlike the condition in *Ophiacodon,* where the neck is less than 20% of the length of the element.

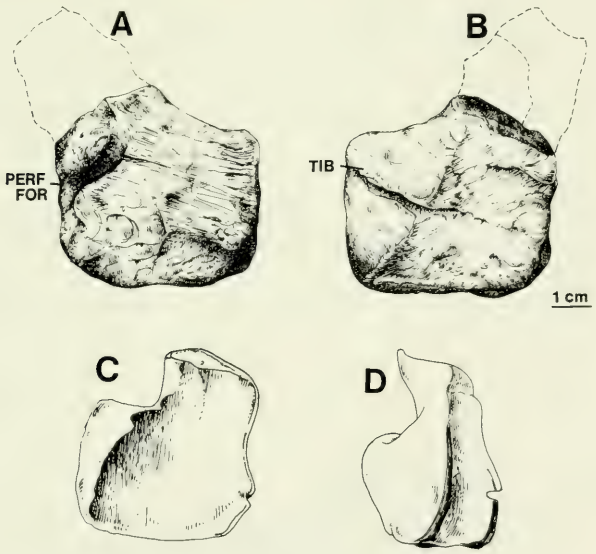


Figure 14. The astragalus of *Stereophallodon* in A) dorsal and B) ventral views, and the astragalus of C) *Ophiacodon* and D) *Dimetrodon. Stereophallodon* drawing based on MCZ 6618. The shaded area is the preserved portion of the right astragalus; the dotted outline is based on the preserved portion of the left astragalus. *Ophiacodon* and *Dimetrodon* from Romer and Price (1940).

Abbreviations: PER FOR, medial edge of perforating foramen, TIB, articular surface for tibia.

Baldwinonus

A fragmentary right maxilla is preserved and displays 25 teeth or alveoli including two that are greatly enlarged (Fig. 15). In lateral view the ventral edge of the maxilla is nearly straight posterior to the caniniform teeth and shows a steep incline anterior to them. No edentulous step is present as in sphenacodontines. The bases of five precaniniform teeth are present. These increase in size posteriorly. All were apparently erupted at the time of death. The base of one caniniform tooth is present and is suboval in cross section with a shallow dorsoventral groove along its anterior and posterior surfaces. The base of this tooth is nine times greater in cross-sectional area than those of the adjacent teeth as originally observed by Romer and Price, 1940. Eighteen postcaniniform teeth or alveoli are present. Those teeth that are fully preserved show compression and recurvature only at the tips. Slight uncrenulated cutting edges are present along these tips.

In medial view, the alveolar ridge is swollen above the caniniform teeth forming a caniniform-tooth buttress. This swelling accommodates the sockets for the caniniform teeth. A horizontal cross section of the dorsal-most extent of the buttress is triangular in outline and thus indicates that the buttress extended dorsad against the medial surface of the maxillary wall as a vertical rod or ridge. Such a

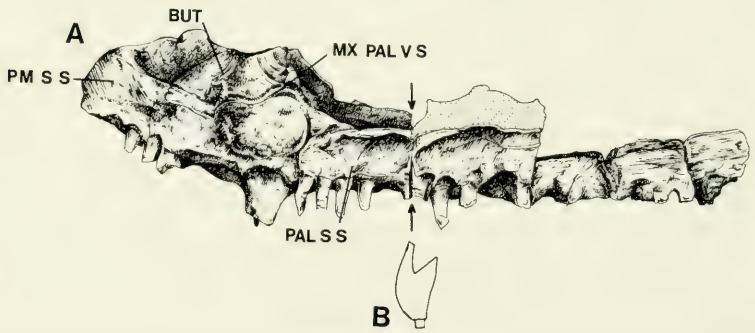


Figure 15. A) the right maxilla of *Baldwinonus* in internal view. Arrows mark the position of B) cross-section through the maxilla. Drawing of AMNH 4780.

Abbreviations: BUT, caniniform buttress; MX PAL V S, maxillary/palatine vessel scar; PAL S S, palatine sutural surface; PM S S, premaxilla sutural surface.

structure is seen in *Ophiacodon* but not in the sphenacodontines where the caniniform-tooth buttress extends dorsally as a broad smoothly contoured wedge. The presence of a rodlike extension is also indicated by the down turning of the maxillary/palatine vessel scar as it passes forward along the medial surface of the buttress. An identical condition exists in *Ophiacodon* where the maxillary palatine vessel is downturned presumably to avoid contact with the edges of the rodlike extension. In sphenacodontines, where the buttress swelling smoothly extends into adjacent surfaces over a broad area at its dorsal terminus, the vessel scar extends forward with no downturning.

Posterior to the buttress the aveolar ridge contracts, forming, in cross section, a V-shaped structure (Fig. 15B). In sphenacodontines, the alveolar ridge remains rectangular in cross section.

The medial half of a left quadrate is preserved (Fig. 16). The articular surface is a saddle-shaped joint. The articular surface of the medial condyle is developed only on its lateral-facing surface. The lateral condyle is not fully preserved. The stapedial pit contains a strong tuberosity, presumably marking the site of contact with the stapes. A notch is present on the dorsal edge of the bone. In all these features, the quadrate of *Baldwinonus* is like that of *Stereophallodon*.

Thirteen partial vertebrae are present. Each can be placed in one of three groups defined on the basis of the morphology of the centrum and transverse process, and the relative position of these

Figure 16. The left quadrate of *Baldwinonus* in posterior, medial, and articular views. Drawing based on AMNH 4780.

Abbreviations: LAT CON, lateral condyle; MED CON, medial condyle; NOTCH, notch in dorsal edge of quadrate; S, stapedial pit.

groups can be established on the basis of comparison with *Stereophallodon*.

The first group comprises four vertebrae; each possesses a sharp, ventral keel, a wedge-shaped cross section, and a bevelled anteroventral edge. This group is represented by the specimen illustrated in Figure 17A. When preserved, the transverse process slopes posterolaterally and is about equal in length to the width of the centrum. It has a large oval articular surface for the rib. The neural spine, preserved on an unillustrated specimen measures about twice the height of the centrum. The slope of the transverse process indicates that these vertebrae are located in the cervical region of the vertebral column.

The second group comprises three vertebrae, two of which are illustrated, Figure 17B and C. These vertebrae are longer than those of the first group and possess a centrum whose ventral surface displays two, close-set parallel ridges. A transverse process, preserved on one of these, is a short laterally directed structure with a ventral buttress extending to the anterior end of the centrum. These vertebrae correspond to the anterior dorsal vertebrae of *Stereophallodon*.

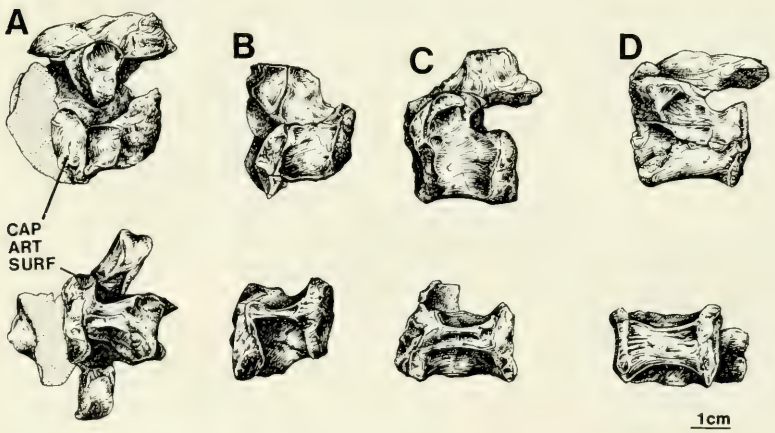


Figure 17. Presacral vertebrae of *Baldwinonus*. A) anterior cervical vertebra, B) mid-cervical vertebra, C) posterior-cervical vertebra, and D) dorsal vertebra. Drawings based on AMNH 4780.

Abbreviations: CAP ART SURF, capitular articular surface.

Six vertebrae constitute the third group and are best exemplified by the illustrated specimen, Figure 17D. These vertebrae possess smooth, flat ventral surfaces. The lateral surfaces of the ventral half of the centra are approximately parallel dorsoventrally, and thus the centra are subrectangular in cross section. These vertebrae correspond to the dorsal vertebrae of *Stereophallodon*.

DISCUSSION

Ophiacodon and *Stereophallodon*

In the review of pelycosaurs presented by Brinkman and Eberth, (1983) two major clades were recognized. The first includes *Casea, Ruthiromia, Varanops,* and *Aerosaurus*. This clade is referred to below as the *Casea-Varanops* clade. It was defined on the basis of three derived character-states: 1) the presence of a secondary ridge leading from the distal end of the deltopectoral crest to a more medial position on the proximal end of the humerus; 2) the presence of a contact between the maxilla and quadratojugal with these bones raised to form a ridge along the contact and; 3) the presence of basipterygoid processes directed laterally and articular surfaces elongate mediolaterally. The second includes *Ophiacodon, Edaphosaurus, Dimetrodon,* and *Sphenacodon*. This clade is referred to below as the *Ophiacodon-Dimetrodon* clade. It is defined on the basis of four shared derived characters: 1) a concave ventral cheek margin; 2) a posteriorly sloping anterior margin of the premaxilla; 3) a dorsal process of the stapes that articulates with the ventral surface of the paroccipital process of the opisthotic and; 4) an extended ventral plate of the angular in the region of the articular.

The *Stereophallodon* material at hand includes only one of the skeletal regions used in defining the *Casea-Varanops* clade (the basipterygoid processes of the basi-parasphenoid). In *Stereophallodon* the processes extend ventrad and possess smooth anteroposteriorly elongate articulating surfaces. Such a morphology is absent in members of the *Casea-Varanops* clade and had been considered a unique derived character of *Ophiacodon* (Brinkman and Eberth, 1983).

The present *Stereophallodon* material includes two of the four skeletal regions used in defining the *Ophiacodon-Dimetrodon* clade (the premaxilla and the angular). The premaxilla is like those of members of the *Ophiacodon-Dimetrodon* clade in that it does not

project anteriad as is the case primitively in pelycosaurs. The angular shares with those of members of the *Ophiacodon-Dimetrodon* clade the presence of an extended ventral plate in the region of the articular. Thus these character-states indicate that *Stereophallodon* is a member of the *Ophiacodon-Dimetrodon* clade.

Within the *Ophiacodon-Dimetrodon* clade, *Stereophallodon* is most parsimoniously placed as the closest sister-taxon of *Ophiacodon* (Fig. 18) and forms with *Ophiacodon* a monophyletic taxon defined by five characters. Two of these, the ventral orientation of the basipterygoid processes and the antero-posteriorly oriented articular surfaces have been discussed above and are present elsewhere in pelycosaurs only in *Ophiacodon.*

Three additional features not discussed by Brinkman and Eberth (1983) can be interpreted as derived and shared by only *Ophiacodon* and *Stereophallodon.* In interpreting the polarity of these characters, the methodology used in Brinkman and Eberth (1983) was employed. The outgroups used are, 1) members of the *Casea-Varanops* clade, which is the closest sister-taxon of the *Ophiacodon-Dimetrodon* clade and, 2) the taxa that were used as outgroups in interpreting the polarities of character-states within pelycosaurs. The polarity of character-states was interpreted according to the distributions shown in Brinkman and Eberth (1983: Fig. 2).

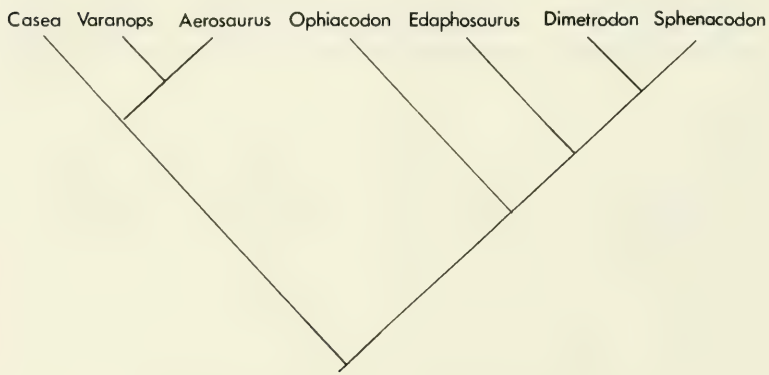


Figure 18. Cladogram showing the interrelationships of seven genera of pelycosaurs. From Brinkman and Eberth (1983).

One of these features is the presence of a ridge that is triangular in cross section extending dorsally from the caniniform-tooth buttress. This is not present in *Edaphosaurus* or the sphenacodontines. The condition is not known in the members of the *Casea-Varanops* clade, but in other reptiles used as outgroups, including *Paleothyris, Captorhinus,* and *Diadectes,* no ridge is present. Thus the absence of such a ridge is interpreted as primitive for pelycosaurs, and its presence is interpreted as a derived feature. Since it is only known in *Stereophallodon* and *Ophiacodon,* it supports the hypothesis that these genera are members of the same clade.

The second feature is the presence of a notch on the posteromedial edge of the quadrate. Although differing in detail, the similarity in position of this and the shelf on the medial surface of the quadrate of *Ophiacodon* indicates that they are different variants on a single character-state. No other pelycosaur shows a notch or shelf in this position. None is present in captorhinids or diadectomorphs. The absence of such a notch, therefore, is interpreted as primitive for pelycosaurs, and the condition in *Stereophallodon* and *Ophiacodon* is interpreted as a derived character-state shared by those two genera.

The third character-state is the presence of a cultriform process that is wide in cross section. In *Dimetrodon, Edaphosaurus, Varanops, Casea,* and *Diadectes,* the cultriform process is bladelike (that is, much higher than it is wide) in cross section. In *Stereophallodon* and *Ophiacodon,* the cultriform process is wider than it is high and has a broad U-shaped cross section. The presence of the bladelike cultriform process in both the members of the *Casea-Varanops* clade and in *Diadectes* indicates that it is primitive for pelycosaurs. The wide cultriform process is therefore interpreted as a derived character state that is shared by *Stereophallodon* and *Ophiacodon.*

An alternative hypothesis of relationship that would place *Stereophallodon* as a member of the *Dimetrodon-Sphenacodon* clade is weakly supported by two characters: the presence of an enlarged caniniform-teeth buttress and two greatly enlarged caniniform teeth. Although the *Dimetrodon-Sphenacodon* clade was not discussed by Brinkman and Eberth (1983), a number of shared derived characters have been cited by Reisz (1980) and Reisz (in press) as defining the clade. These are the presence of 1) an

edentulous step anterior to the caniniform teeth; 2) enlarged caniniform teeth; 3) a swollen caniniform tooth buttress; 4) a reflected lamina of the angular; 5) a tall septomaxilla; 6) keeled dorsal vertebrae; 7) a ventrolaterally oriented paroccipital process; 8) a short lacrimal; 9) a tall skull and; 10) a strongly convex maxillary margin. The absence in *Stereophallodon* of an edentulous step anterior to the caniniform teeth, a reflected lamina, keeled dorsal vertebrae, and ventrolaterally oriented paroccipital processes indicates that *Stereophallodon* cannot be a member of this clade. Furthermore the absence in *Stereophallodon* of characters that define the *Edaphosaurus-Dimetrodon-Sphenacodon* clade (basipterygoid articular surfaces at right angles; absence of a shelf between the basipterygoid tubera, a well-developed lateral lappet of the frontal, a downturned prearticular, a pterygoideus process formed by the articular, a quadrate ramus of the pterygoid without a tympanic flange, a well-developed lateral process of the supraoccipital, lateral excavations on the neural arches, transverse processes of vertebrae lacking a ventral web of bone) indicates that *Stereophallodon* is not the sister taxon of the *Dimetrodon-Sphenacodon* clade. Thus *Stereophallodon* is interpreted as the closest sister-taxon of *Ophiacodon* that has paralleled members of the *Dimetrodon-Sphenacodon* clade in the development of enlarged caniniform teeth supported by a large caniniform-tooth buttress. This hypothesis of relationship is in agreement with the recommendation of Reisz (1980) that *Stereophallodon* be separated from the Eothyrididae and placed in the Ophiacodontidae.

In some characters, *Stereophallodon* and *Ophiacodon* are different. Outgroup comparison was used to determine whether the character-states that occur in *Stereophallodon* are primitive for the *Ophiacodon-Stereophallodon* clade or apomorphic for *Stereophallodon*. The outgroups used in this analysis are the *Edaphosaurus-Dimetrodon* clade (the sister-taxon of the *Ophiacodon-Stereophallodon* clade), the *Casea-Varanops* clade (the sister-taxon of the *Ophiacodon-Dimetodon* clade), other reptiles (the sister-taxon to the pelycosaurs) and diadectomorphs (the sister-taxon to all of these). The polarity of character-states was interpreted according to the distributions shown in Brinkman and Eberth (1983: Fig. 2).

One of the differences between *Stereophallodon* and *Ophiacodon* is in the structure of the centra. In *Stereophallodon* the dorsal

vertebrae are rectangular in end view, and have flat ventral surfaces and subparallel sides. In *Ophiacodon* vertebrae of the cervical and dorsal region are wedge-shaped in cross section and vertebrae of the lumbar region are circular in end view and in cross section. The dorsal vertebrae of *Casea* are like those of *Stereophallodon*. Those of *Ruthiromia* differ in detail, but are similar to *Stereophallodon* in that the posterior dorsal vertebrae tend to have a flat ventral surface. Also, the trefoil shaped cross section seen in the lumbar vertebrae of *Stereophallodon* can be considered a structural antecedent to the "pinched-in" condition of the lumbar vertebrae of *Ruthiromia* (see Eberth and Brinkman, 1983). Since *Casea* and *Ruthiromia* are primitive members of the *Casea-Varanops* clade, and *Stereophallodon* is primitive within the *Ophiacodon-Dimetrodon* clade, the morphology of the centra of the dorsal vertebrae seen in *Stereophallodon* is interpreted as primitive with respect to *Ophiacodon*. Inherent in this conclusion is the interpretation that this centrum morphology is primitive for pelycosaurs.

A second difference between *Stereophallodon* and *Ophiacodon* is seen in the structure of the femur. The femur of *Ophiacodon* possesses a sharp adductor crest that runs along its postero-ventral edge. *Stereophallodon* differs from *Ophiacodon* and is like other pelycosaurs in that the adductor crest is located in a mid-ventral position. The wide distribution of this latter character-state indicates that it is a primitive feature in pelycosaurs. Thus in this feature, *Stereophallodon* is more primitive than *Ophiacodon*.

A third difference between *Stereophallodon* and *Ophiacodon* is seen in the structure of the astragalus. In *Stereophallodon* the astragalus has a long neck, in *Ophiacodon* it is short. The astragalus of *Ophiacodon* has been thought to be primitive, but establishing polarities has been difficult (Eberth and Brinkman, 1983). A long neck is present in *Ruthiromia* (the primitive member of the *Varanops* clade), *Edaphosaurus* (the primitive member of the *Edaphosaurus-Sphenacodon-Dimetrodon* clade), and *Stereophallodon*. Thus the *Stereophallodon* character-state is interpreted as the primitive condition for pelycosaurs.

A fourth difference between *Stereophallodon* and *Ophiacodon* is seen in the structure of the quadrate. The quadrate of *Stereophallodon* is distinctive in the shape of the articular surface. *Edaphosaurus, Ophiacodon,* the sphenacodontids, *Casea,* and the varanopseids

each have a different quadrate articular morphology. Thus it is not possible to determine which is the primitive pattern using outgroup comparison.

A fifth difference between *Stereophallodon* and *Ophiacodon* is seen in the structure of the fibula. The fibula of *Stereophallodon* is distinctive in the triangular cross-sectional shape of its proximal end. In *Ophiacodon,* the fibula has a rectangular proximal end. This is also the case in *Edaphosaurus,* sphenacodontines, and the varanopseids. Thus the character-state seen in *Ophiacodon* is interpreted as the primitive character-state and that seen in *Stereophallodon* is considered apomorphic for that genus.

Finally, *Stereophallodon* differs from *Ophiacodon* in the presence of a caniniform-tooth buttress and the large size of the caniniform teeth. As discussed above, these are interpreted as derived features acquired in parallel with the derived members of the *Dimetrodon-Sphenacodon* clade.

In summary, *Stereophallodon* is interpreted as the closest sister-taxon of *Ophiacodon.* Its position in the *Ophiacodon-Edaphosaurus-Dimetrodon* clade is supported by seven shared derived character-states. Two of these are shared with all other members of the clade; five are derived features shared only with *Ophiacodon.* The two features shared with all other members of the clade are the presence of a platelike extension of the angular beneath the articular and the posterior slope of the dorsal ramus of the premaxilla. The features that unite *Stereophallodon* with *Ophiacodon* are the shape of the cultriform process of the basi-parasphenoid, the ventrally directed basipterygoid process, the anteroposteriorly oriented basipterygoid articular surfaces, the presence of a ridge that is triangular in cross section extending dorsally from the caniniform-tooth buttress, and the presence of a notch on the postero-medial edge of the quadrate. *Stereophallodon* shares five features with *Ophiacodon* that are primitive relative to *Edaphosaurus* and the sphenacodontines. These are the presence of a triangular process located medial and anterior to the articular, the presence of a tympanic flange on the ventral edge of the quadrate ramus of the pterygoid, the absence of an anterior process on the ilium, the presence of a shelf covering the anterior end of the groove between the basisphenoid wings, and the absence of a retroarticular process. *Stereophallodon* is primitive with respect to *Ophiacodon* in retaining the following characters:

dorsal vertebrae that have flattened ventral surfaces and subparallel sides, a femur with an adductor crest running along the mid-ventral surface of the bone, and a long neck on the astragalus. *Stereophallodon* is derived relative to *Ophiacodon* in the presence of two greatly enlarged caniniform teeth supported by a caniniform-tooth buttress, and a fibula that has a triangular cross section at its proximal end.

Baldwinonus

Before considering the systematic position of *Baldwinonus* it is necessary to consider whether or not more than one individual is present in the type specimen. This was questioned by Reisz (1980), who identified the centra as ophiacodont elements, and the maxilla and neural spines as sphenacodont. Thus Reisz concluded that at least two individuals were present.

In identifying the maxilla as that of a sphenacodont, rather than a sphenacodontine—the only group of sphenacodonts known from New Mexico—Reisz recognized that it differs significantly from the maxilla of other better known sphenacodontines. Also, in identifying the vertebrae as ophiacodont vertebrae Reisz recognized that they were not from *Ophiacodon,* the only ophiacodontid present in New Mexico. In the features in which the vertebrae and maxilla of *Baldwinonus* are different from the sphenacodontines and *Ophiacodon,* they are like *Stereophallodon.* The quadrate of *Baldwinonus,* not considered by Reisz, is also like *Stereophallodon* and unlike the quadrate of *Ophiacodon* or the sphenacodontines. While studying the type specimen, it was possible to piece together many of the vertebral fragments. Some of the resulting vertebrae are in articulation, and in one case a neural spine, identified as a sphenacodont neural spine by Reisz, could be attached to a centrum. Thus, it is concluded that the type specimen of *Baldwinonus* is most probably a single individual that is morphologically similar to *Stereophallodon.*

In most features in which both *Baldwinonus* and *Stereophallodon* are known, *Baldwinonus* is simply a smaller version of *Stereophallodon.* A difference in the structure of the maxilla is present: in *Stereophallodon,* the palatine sutural surface extends onto the caniniform-tooth buttress; in *Baldwinonus,* the palatine sutural surface ends just posterior to the caniniform-tooth buttress. On the basis of this difference, *Baldwinonus* is considered a valid genus.

Two derived character-states that unite *Stereophallodon* and *Ophiacodon* are also present in *Baldwinonus;* therefore, the three genera can be combined in a monophyletic group. These are the presence of the rodlike dorsal extension of the caniniform-tooth buttress on the internal surface of the maxilla and the presence of a notch in the postero-medial surface of the quadrate.

That *Baldwinonus* and *Stereophallodon* may be more closely related to each other than either is to *Ophiacodon* is indicated by the shared derived character-state of greatly enlarged caniniform teeth supported by a buttress on the internal surface of the maxilla. Other character-states of *Stereophallodon* that were interpreted as being derived, specifically the structure of the proximal end of the fibula, are not known in *Baldwinonus.*

Character-states shared by *Baldwinonus* and *Stereophallodon* that can be considered primitive for pelycosaurs in general are seen in the structure of the vertebrae. The vertebrae of *Baldwinonus* are like those of *Stereophallodon* in that the dorsal vertebrae have flat ventral surfaces and subparallel sides. Thus the discussion of the polarity of the vertebral features of *Stereophallodon* given above also applies to *Baldwinonus.*

The structure of the maxilla of *Baldwinonus* is more fully known than that of *Stereophallodon.* Like the maxilla fragments of *Stereophallodon,* it is only superficially similar to the sphenacodontines. The differences include the absence of the following derived sphenacodontine characters: a maxillary step, a reduced tooth count, compressed teeth with fully developed cutting edges, an evenly tapering caniniform-tooth buttress, and a rectangular post-buttress alveolar ridge.

In summary, from the characters discussed here, it is concluded that *Baldwinonus* is closely related to *Stereophallodon.* These genera are interpreted as primitive members of a clade that also includes *Ophiacodon,* and therefore replace *Ophiacodon* as the most primitive known member of the *Ophiacodon-Dimetrodon* clade (Fig. 19). Character-states shared by *Stereophallodon, Baldwinonus,* and primitive members of the *Casea-Varanops* clade can be considered primitive for pelycosaurs. One such feature is the structure of the centra of the dorsal vertebrae. This is of significance in providing evidence that pelycosaurs, as traditionally defined, had a monophyletic origin.

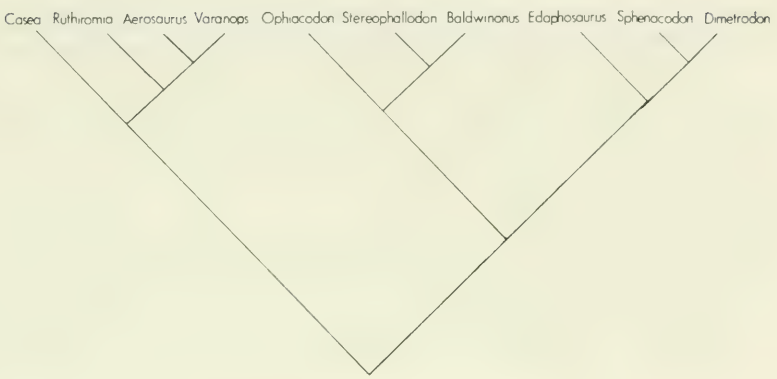


Figure 19. Cladogram showing the interrelationships of *Stereophallodon, Baldwinonus* and the pelycosaurian genera considered by Brinkman and Eberth (1983) and Eberth and Brinkman (1983).

ACKNOWLEDGMENTS

The authors are greatly indebted to the scientific and curatorial staff of the American Museum of Natural History for permission to study specimens in their care. The manuscript was read by Phil Currie. His critical comments were greatly appreciated. The specimen drawings, except for Figures 1C–E, 5, and 7A–B, were made by Linda Krause of the Tyrrell Museum of Palaeontology. Figures 1C and 7A–B were made by Donna Sloan of the Tyrrell Museum. The manuscript was typed by Judy McMillan. The comments of two anonymous reviewers also greatly improved the manuscript. The responsibility for any errors in methodology or conclusion rest solely with the authors.

LITERATURE CITED

Brinkman, D. B., and D. A. Eberth. 1983. The interrelationships of pelycosaurs. Breviora No. 473, 35 pp.

Eberth, D. A., and D. B. Brinkman. 1983. *Ruthiromia elcobriensis,* a new pelycosaur from El Cobre Canyon, New Mexico. Breviora, No. 474, 26. pp.

Langston, W., Jr. 1965. *Oedaleops campi* (Reptilia: Pelycosauria). A new genus and species from the Lower Permian of New Mexico and the family Eothyrididae. Bull. Texas Mem. Mus., **9:** 1–46.

Reisz, R. R. 1980. The Pelycosauria: a review of phylogenetic relationships, pp. 553–592. *In* A. L. Panchen (ed.), The Terrestrial Environment and the Origin of Land Vertebrates, London and New York, Academic Press.

———. Pelycosauria. Handbuch der Palaeoherpetologie. Fischer, Stuttgart.

Romer, A. S. 1937. New genera and species of pelycosaurian reptiles. Proc. New Engl. Zool. Club, **16:** 89–96.

Romer, A. S., and L. I. Price. 1940. Review of the Pelycosauria. Geol. Soc. Am. Spec. Pap. No. 28, 538 pp.

Vaughn, P. P. 1958. On a new pelycosaur from the Lower Permian of Oklahoma, and the origin of the family Caseidae. J. Paleont., **32:** 981–991.

Watson, D. M. S. 1954. On *Bolosaurus* and the origin and classification of reptiles. Bull. Mus. Comp. Zool., **111:** 299–249.

———. 1957. On *Millerosaurus* and the early history of the sauropsid reptiles. Phil. Trans. Roy. Soc. Lond., B, **240:** 325–400.

BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 29 AUGUST 1986 NUMBER 486

THELODUS MACINTOSHI STETSON 1928, THE LARGEST KNOWN THELODONT (AGNATHA: THELODONTI)

SUSAN TURNER[1]

ABSTRACT. Material attributed to the thelodont *Thelodus macintoshi* Stetson, from the Silurian of New Brunswick, Canada, is shown to be heterogeneous. It comprises not only the type thelodont, *T. parvidens* Agassiz 1839, but also a species of *Loganella* similar to *L. ludlowiensis* or *L. martinssoni* (Gross 1967) and an acanthodian resembling *Gomphonchus*. Scales of *T. bicostatus* Hoppe and *T. trilobatus* Hoppe are found in association with those of *T. parvidens* for the first time. Measurements of Stetson's type material confirm that *T. parvidens* is the largest known thelodont, with a total length of about one meter. The vertebrate fauna including these thelodonts could be as old as late Llandovery (within the Long Reach Formation) or as young as early Pridoli (in the Jones Creek Formation). The New Brunswick thelodonts are similar in preservation to those from the Lower Silurian fish beds of Scotland, but their phylogenetic affinities are closer to those from the Silurian of England and the Baltic region.

INTRODUCTION

In 1928 Harold Stetson described articulated thelodont material, preserved in calcareous concretions, from a site in the Silurian rocks near Nerepis, Kings Co., New Brunswick, eastern Canada. This was the first definite thelodont material found in North America. The site, at Cunningham's Brook (Cunningham's Creek on the map of MacKenzie 1964), has also yielded the heterostracan *Cyathaspis acadica* (Matthew), (see Denison 1964), spines of an acanthodian related to *Climatius* (Denison 1956, p. 385), and a possible anaspid,

[1]Queensland Museum, Fortitude Valley, Queensland 4006, Australia

Ctenopleuron nerepisense Matthew 1907, which remains indeterminate (e.g., Woodward 1920). Associated invertebrates include ceratiocarids, conodonts and a xiphosuran (Denison 1956; Blieck 1982).

MATERIALS AND METHODS

The nodules containing this thelodont material were collected from siltstones by Stetson and W. E. Schevill of the Museum of Comparative Zoology during a Harvard expedition in 1927, following up the lead of William MacIntosh of the Natural History Society of New Brunswick. The type material is housed at the Museum of Comparative Zoology, Harvard University.

Subsequently, during the 1950s and 1960s, Robert Denison (then of the Field Museum of Natural History, Chicago) collected more material from two separate horizons. Denison referred all the thelodonts he collected to *Thelodus macintoshi* Stetson. In 1956 he stated that the specimens came from the Long Reach Formation, following the lead of Matthew (1888) who stated that the fish beds were in the Mascarene Group, Division 2 which was subsequently called the Long Reach Formation (e.g., MacKenzie 1951). In 1964 Denison corrected his statement by referring the *Cyathaspis acadica* material to the Jones Creek Formation, on the basis of MacKenzie's 1951 field appraisal. This interpretation was followed by Blieck (1982).

Evidence, however, from the 1964 maps of the region by MacKenzie suggests that all the fish beds are within the older Long Reach Formation. The position of the two formations has been confused because in the 1950s, and on the 1964 Saint John and Hampstead maps, MacKenzie placed the Jones Creek Formation *below* the Long Reach Formation. In fact, the reverse order is the case (Berry and Boucot 1970; McCutcheon 1981). One recent source places the fish beds definitely within the Long Reach Formation (Smith 1966). In the notes of the 1964 Hampstead map there is even a reference to a new locality in the Long Reach Formation for "a primitive fish" in a brook, northeast of Armstrong Corner. This specimen was not identified and I have no further information about it. It may be that the cyathaspids did not come from the same horizon as the thelodonts and other elements of the fauna.

In the early 1970s, Denison sent me, on request, a sample of loose scales from one of the nodules from the New Brunswick site. I

attempted to make thin sections, but the histological structure of the scales was disrupted by post-mortem algal or fungal attack, or recrystallization (see Pl. 1). In general shape, however, the scales seemed identical to those of *T. parvidens*. I also examined a specimen of *T. macintoshi* in the British Museum (Natural History), collected from New Brunswick by W. Graham-Smith in 1937. On the basis of these investigations, I suggested that *T. macintoshi* was virtually identical to *T. parvidens*, at least in its scale morphology (Turner 1973, 1976). [I also stated that the Long Reach Formation was the stratotype, following Denison 1956; see also Blieck 1982]. From a perusal of Stetson's figures in 1968 I decided to write a paper on the closure of Iapetus, the early Palaeozoic ocean (Turner 1970). For if *T. parvidens* and *T. macintoshi* were the same species, then New Brunswick and the Anglo-Welsh region must have been closely aligned in the late Silurian.

In his original work Stetson (1928, Figs. 1–3) described and figured scales he thought looked like typical *T. parvidens* scales but which bore long thin extensions on the posterolateral rims of the crowns (Figs. 2, 3). This character prompted him to distinguish *T. macintoshi* as a separate species. In spring 1983 I examined both Stetson's and Denison's collections. Specimens PF are housed at the Field Museum of Natural History, Chicago (FMNH), MCZ at the Museum of Comparative Zoology, and BMNH at the British Museum of Natural History.

MATERIALS EXAMINED

MCZ 2035	HOLOTYPE *Thelodus macintoshi* Stetson 1928 is *T. parvidens* Agassiz with *T. trilobatus* scale. Area at least 30 + × 250 mm. Holotype includes thin sections.
MCZ 2037	Paratype *T. macintoshi* is *T. parvidens*.
MCZ 2036	Paratype *T. macintoshi* is *Loganella* cf. *L. ludlowiensis* (Gross 1967).
MCZ 13007	in part to 13015, includes the specimens from which some thin sections were cut, are referred to *T. parvidens* Agassiz.
MCZ 13007	in part; one nodule has *Gomphonchus* type scales.
MCZ 13014	includes *T. bicostatus* (Hoppe 1931) scales.
MCZ 13012	is at least 240 mm long.

PF 1805 *T. macintoshi* is *T. parvidens,* area 300 × 170 mm (Denison coll.).

PF 1809 *T. macintoshi* is *T. parvidens* horizon A, area at least 300 × 170 mm (Denison coll.).

PF 1804 *T. macintoshi* is *T. parvidens,* horizon B (Denison coll).

PF 1808 loose thelodont scales in coprolite includes *T. parvidens, T. bicostatus* and *T. trilobatus,* horizon B.

PF 1803 is a coprolite containing *Gomphonchus* type scales.

PF 1802 is a coprolite with thelodont scales, *T. parvidens,* horizon B.

PF 3475 jumbled *T. parvidens* scales in coprolite, (Denison coll. 1961).

PF 3476 *T. macintoshi* - a good articulated *T. parvidens,* incomplete 150 × 90 mm in area (Denison coll. 1961).

PF 3477 and PF 1801 are acanthodians and PF 1698 is an acanthodian ?spine. At least three uncatalogued specimens, including 126-52 and 1969 Denison coll. FMNH, are coprolites from horizon B containing well-preserved *T. parvidens* scales.

BMNH P.52444. *T. macintoshi* (Graham-Smith coll.) is *T. parvidens* with *T. trilobatus*? scales.

Plate 1. Histology of thelodont scales from coprolitic nodules from Cunningham's Brook, Nerepis, New Brunswick (slides prepared at Field Museum, Chicago). A) Vertical section through large scales of *T. parvidens* showing growth lines in orthodentine and invading hyphae or boring algae; anterior to left, slide 4187; B) Small scale of *T. parvidens* in sagittal section interposed between two larger scales of *T. parvidens,* slide 4187; C) Sagittal section through a scale of *T. parvidens* with a much enlarged anterior base (in the manner of *T. laevis* Pander (see Gross 1967; Karatajute-Talimaa 1978), and the pulp canal; anterior to left, slide 4192; D) Young scale of *Thelodus trilobatus* with large open pulp cavity, in sagittal section; anterior to right, slide 4192; E) Scale of *Thelodus bicostatus* in transverse vertical section showing growth lines, slide 4187. F) Scale of *T. bicostatus* or *T. trilobatus* showing growth lines and invading hyphae or algae, slide 4187; G) Horizontal section through crown of *T. parvidens* scale, slide 4192. All to same size, approx. ×60.

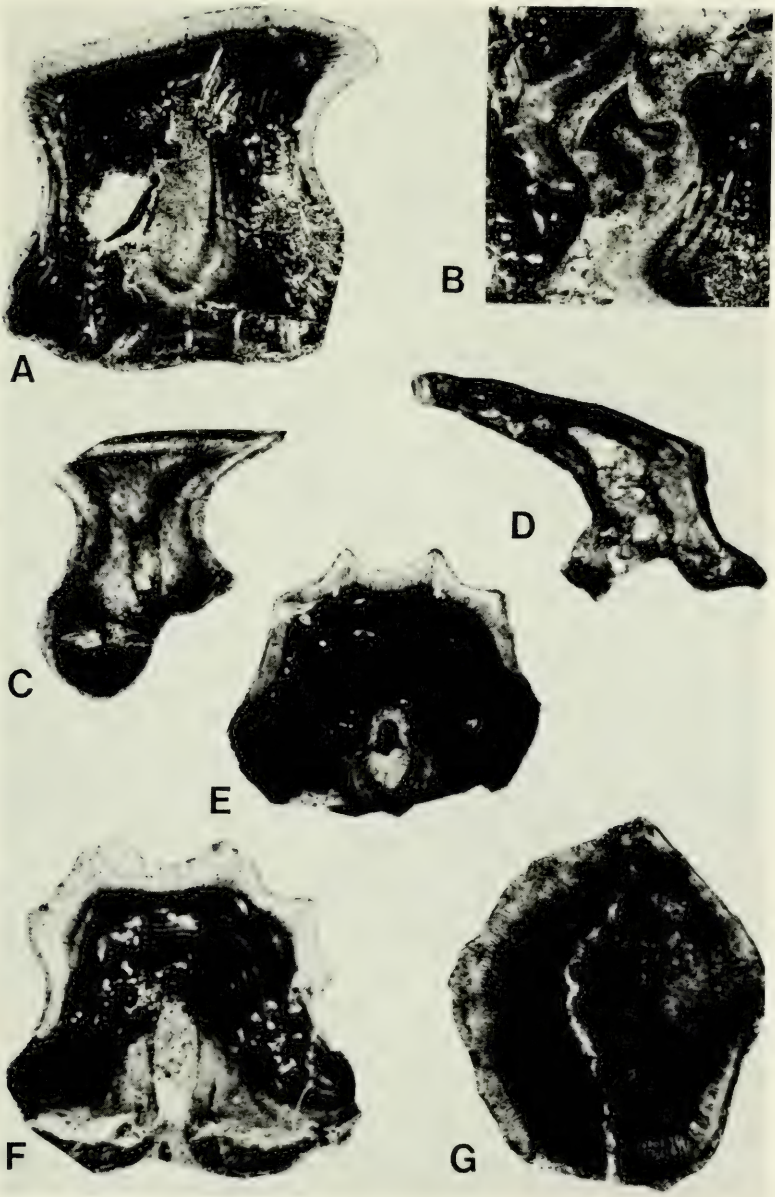

A
B
C
D
E
F
G

Figure 1. *Thelodus macintoshi* Stetson 1928 = *Thelodus parvidens* Agassiz 1838. Holotype, MCZ 2035. Close dotting: small *T. parvidens* scales in part, towards the sides of the heart-shaped nodule (probably the region of the pectoral fins). Larger scales in center; good articulated patches shown. Asterisk mark: one scale of *T. trilobatus*. Parallel bars: cracks in the nodule with slickensides. Clear rectangles: specimen labels. Arrow points to anterior.

RESULTS

Material. Examination of Stetson's specimens and his thin sections (to which the 1928 plates do not do justice), and of Denison's material, reveals that the material attributed to *T. macintoshi* is heterogeneous: it comprises at least two genera of thelodonts, and one specimen is actually an acanthodian. *T. macintoshi* (*s.s.*) is almost certainly synonymous with *T. parvidens*. I propose that *T. macintoshi* Stetson should be formally considered a junior synonym of *T. parvidens,* but I shall refer to *T. macintoshi* in an informal sense to distinguish the New Brunswick material from other material.

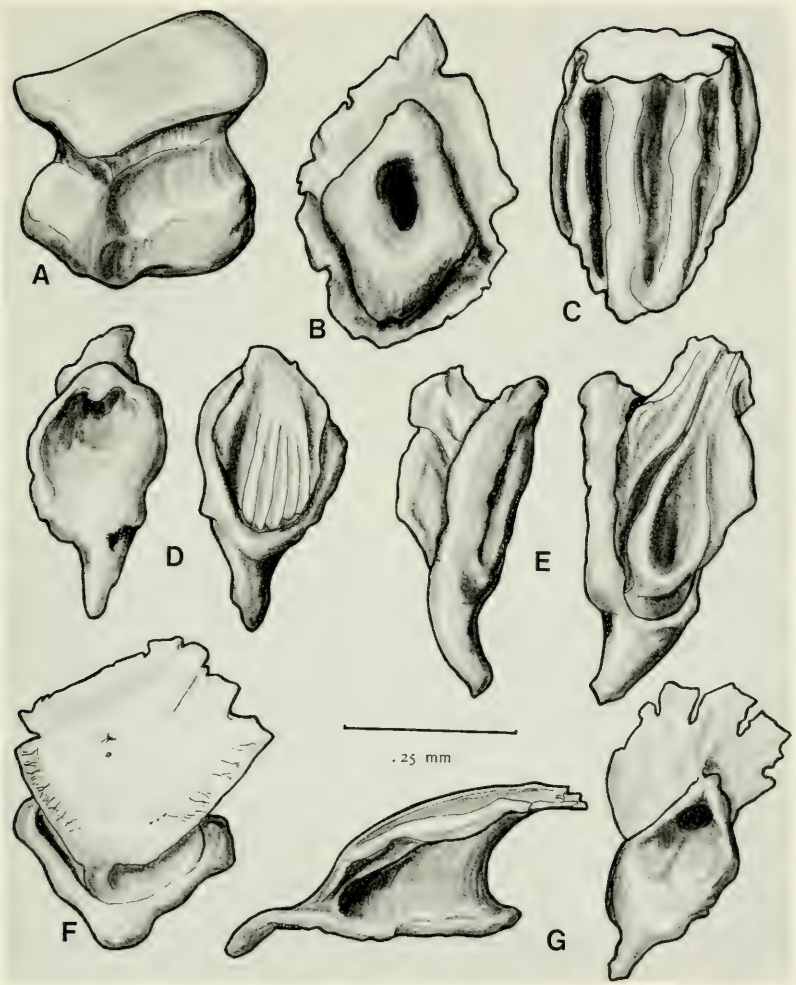


Figure 2. Isolated scales from nodule PF 9603 from horizon B of Denison, Cunningham's Brook, Nerepis, New Brunswick. A) *T. parvidens,* lateral view showing neck riblets, PF 9603.1; B) *T. parvidens,* ventral view, PF 9603.2; C) *T. bicostatus,* dorsal view of broken crown, PF 9603.3; D) *T. trilobatus,* ventral and dorsal views, PF 9603.4; E) *T. trilobatus,* lateral and dorsal views, PF 9603.5; F) *T. trilobatus,* dorsal view of smooth crown, PF 9603.6; G) *T. trilobatus,* lateral and ventral views, PF 9603.7.

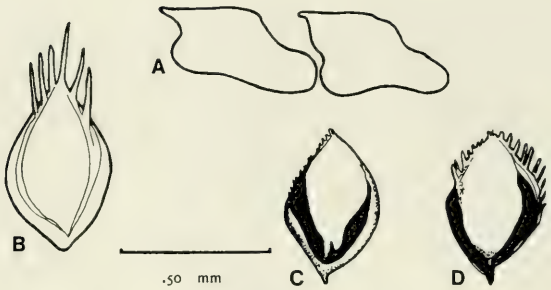


Figure 3. Scales on paratype of *T. macintoshi,* MCZ 2036. A) *Loganella* sp., two scales seen in cross section; B) *Loganella* sp., body scale in crown view showing unbroken posterolateral spinelets; C–D) *Loganella* sp., body scales in crown view with small anterior basal process and posterolateral neck spinelets.

The scales of the *T. macintoshi* specimens are large, up to 1.5 mm long, and in an advanced stage of growth with well-developed bases (see Fig. 2A, Pl. 1A–C); they are undoubtedly scales of a mature animal. They differ from European examples of *T. parvidens* (including the type specimen) in the clear expression of the numerous riblets on the neck region (Pl. 2). However, as most European scales are waterworn to some degree it seems possible that the full extent of neck ribbing in the type species has never been clearly seen in the isolated scales. Gross did show one scale with 12 riblets on one side of the neck (1967, Pl. 1, Fig. 3A) but their number is usually much smaller. The slight differences in rib ornament on the neck of scales may reflect local variation within a single population of *Thelodus parvidens.*

Furthermore, some of the specimens, including coprolitic masses and thin sections, show that scales of *T. bicostatus* type are part of the *T. parvidens* squamation (see Fig. 2). Despite the fact that the scales of *T. bicostatus* are very distinctive, both Gross (1967) and Turner (1973, 1976) thought they might be special scales of *T. parvidens,* while retaining the specific name *bicostatus.* One scale on the type specimen (MCZ 2035) appears to belong to *T. trilobatus* (see Fig. 1). A patch of small striated scales among the larger rhomboid *T. parvidens* scales on specimen BMNH P52444 could also belong to *T. trilobatus.* Scales of this species are also seen in coprolitic masses (Fig. 2D–G). Thin sections of scales from the nodules

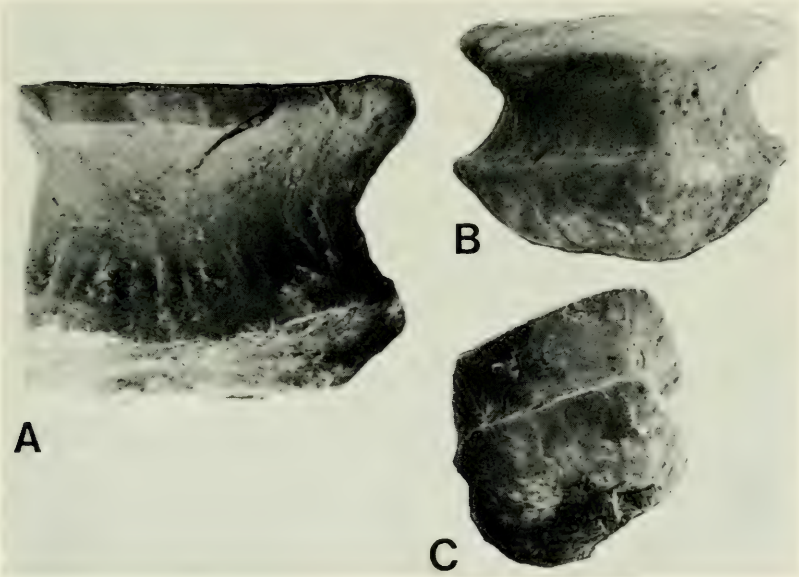


Plate 2. Scales of *Thelodus parvidens* from coprolitic nodule from Cunningham's Brook, Nerepis, New Brunswick. A) Detail of neck in lateral view showing riblets on lower neck, PF 9603.8, approx. ×60; B) Scale in lateral view, PF 9603.8, approx. ×45; C) Scale in posterobasal view showing pulp cavity, PF 9603.10, approx. ×45.

confirm the presence of *T. parvidens* in association with *T. bicostatus* and *T. trilobatus* (see Pl. 1). Thus the *T. macintoshi* material confirms the synonymy of *T. parvidens, T. trilobatus* and *T. bicostatus* postulated initially by Gross (1967).

The most interesting discovery in this re-examination of Stetson's type material is the presence of at least one specimen of a loganiid. The paratype of *T. macintoshi* (MCZ 2036) is not a thelodontidid, but a specimen of *Loganella* sp. cf *L. ludlowiensis* (Gross 1967) or perhaps cf *L. martinssoni* (Gross 1967). [The genus name *Logania* formerly attributed to this and other loganiid species is preoccupied (*Logania* Distant—Lepidoptera; Whitley 1976). Here I propose to use the replacement name *Loganella.*] The figures in Stetson's paper depicting scales with rim spines actually represent sagittal sections through *Loganella* scales (see Fig. 3). The scales in the nodule are sometimes broken through, exposing the slit-like pulp canal and

navicular shape of typical loganiid body scales (cf Gross 1967 e.g., Figs. 11 I–K).

At least two specimens from Nerepis, one in each of the collections at MCZ and the Field Museum, are not thelodonts but acanthodians. The scales are those of an ischnacanthid cf *Gomphonchus.*

It is not really difficult to see why Stetson did not recognise the different thelodonts in his fauna. Before 1928 only a few cross-sections of *Thelodus* scales, except those of *T. parvidens,* had been illustrated. Knowledge of the histological structure of scales did not become refined until the comprehensive study by Gross (1967), in which he separated the genus *Logania* from *Thelodus.* The MCZ houses the thin sections Stetson used; those cut from MCZ 2036 show the teardrop-shaped outlines of *Loganella* scales cut in horizontal section, with a slit-like pulp cavity. Nine slides of nodule pieces containing scales of *T. macintoshi* are housed at the Field Museum.

In the main, these scales are well-preserved and the sections show clearly that the scales belong to *T. parvidens*: some sections of the scales are mere "ghosts," the internal structure of the dentine having been recrystallised. One slide, PF slide 4187/52-102b, contains cross-sections of two scales of *T. bicostatus* (Hoppe 1931) (see Pl. 1E). Many of the scales of *T. parvidens,* including the *bicostatus* and *trilobatus* forms, exhibit clear incremental lines in the dentine; there are from nine to 11 in large scales and two to three in small scales (see Pl. 1). The incremental lines in thelodont scales are a measure of scale growth (Gross 1967). Whether the lines represent annual or seasonal increments may never be ascertained; if the animals were living in warm near-equatorial waters, as has been suggested for Siluro-Devonian vertebrates on other occasions (e.g., Halstead and Turner 1973), then it seems possible that the lines represent seasonal fluctuations in the availability of calcium and/or phosphate. Some scales are also penetrated by what look like fungal hyphae, similar to those described by Goujet and Locquin (1977) and Karatajute-Talimaa (1978) (see Pl. 1A, F).

Size of T. parvidens. Several of the nodules (e.g., those containing the holotype, see Fig. 1) contain articulated squamation which indicates that the thelodonts were very large. Stetson was correct in estimating that *T. macintoshi* was longer than *Turinia pagei* (Powrie

1870), the largest known thelodont at that time. He considered that some eight to ten inches would need to be added to the length of the holotype *Turinia,* making an estimate of 22 inches (around 550 mm) for *T. macintoshi.* Study of the type specimen shows that scales towards the center are very large, around 1.5 mm square, and closely packed in neat diagonal rows, whereas towards the antero-lateral margins the scales are progressively smaller, around 0.5 mm square and along the lateral margins the very small scales are much disrupted (Fig. 1). I suggest that, by comparison with the type specimen of *Turinia pagei* (see Turner 1982), the type specimen exhibits part of the cephalothorax extending to the region of the proximal tips of the pectoral fins. The specimen measures about 300 mm long by 250 mm wide. Given that the cephalothorax was probably about one quarter to one third of total body length, this New Brunswick thelodont might have had a length between 900 and 1200 mm. Other nodules in the collections examined show areas of squamation at least as large as that in the type specimen. With a length around one meter, these specimens of *T. parvidens* are the largest thelodonts found to date. This more than confirms Stetson's prediction about the size of the animals.

Age of the Nerepis fauna. Matthew (1888) considered the fish-bearing beds to be of Niagaran age because of the associated fauna, which includes *Ceratiocaris pusillis* and the xiphosuran *Bunodella horrida* (Denison 1956). Bailey and McInnes (1888) reported that Matthew regarded the beds to be about the same age as those containing *Palaeaspis* in the United States, that is, the Medina and Clinton Groups, and equivalent to Divisions 2 and 3 of the Anticosti Group and Groups B and B^1 of Arisaig. Westoll (1958a) placed the beds within the Wenlock, equivalent to the Lockport of the United States.

Both the Long Reach and Jones Creek Formation beds lie within the Mascarene Group, referred to as the Upper Silurian by the Canadian Geological Survey (MacKenzie 1964). When MacKenzie's maps were published in 1964 it was still not certain whether the Jones Creek Formation lay above, or below, the Long Reach Formation. The latter has been dated as Upper Llandovery/Lower Wenlock (C6), because of its *Costistricklandia-Eocoelia* community (Berry and Boucot 1970). MacKenzie (1951) had placed the Long Reach Formation above the Jones Creek Formation, but Berry and

Boucot, following a statement by MacKenzie, considered that it must rest below and that the Jones Creek Formation was of Ludlow/Pridoli age (see also Blieck 1982). McCutcheon (1981) has reiterated this interpretation, which would imply a large time gap between the two formations. I am not able to ascertain from the literature if this hiatus is discernible in the field. On their correlation chart Berry and Boucot (1970) show the Long Reach Formation extending from ?Upper Llandovery to Ludlow, but based on the brachiopod fauna, they prefer a Late Llandovery/Early Wenlock age. The Jones Creek Formation is possibly as old as Upper Ludlow (Ludfordian), for, as Berry and Boucot point out, the beds contain a *Salopina* community which is thought to signify Ludlow shallow water conditions in the Welsh Borderland (Lawson 1975).

Berry and Boucot compared the Jones Creek Formation with the Pembroke Formation of Maine. Devonian fish material has been discovered in the Eastport Formation of this region by Denison (Field Museum collections) but is not described yet. As the stratigraphy and structure of the Nerepis area seem complex, perhaps a more thorough search for fish remains in equivalent Siluro-Devonian beds nearby in Canada and in the United States would help clarify the succession.

The association of cyathaspids, acanthodians and *T. parvidens* (including *trilobatus* and *bicostatus* varieties) and a *Loganella* sp. cf. *L. ludlowiensis* in New Brunswick could be as old as early Wenlock and no younger than early Downton. A similar assemblage of these thelodont species and acanthodian scales has been found in sediments as old as Lower Wenlock in the Welsh Borderland (Turner 1973) and also in the Upper Llandovery of Norway (Turner 1984), and it is also found throughout the Upper Ludlow and early Downton of Europe (Turner 1973; Karatajute-Talimaa 1978; Märss 1982b). Märss (1982b) suggests that the pre-late Ludlow loganiid in the Welsh Borderland is in fact *L. martinssoni.* The possibility that the New Brunswick loganiid may belong to this latter species cannot be ruled out. Cyathaspidids are known from supposed Upper Llandovery and Wenlock sequences in the Canadian Arctic but details of these early forms are not yet published (Denison 1964; Thorsteinsson 1967; Dineley and Loeffler 1976). In their review of cyathaspids Dineley and Loeffler (1976) compared *Cyathaspis acadica* with *C. banksi,* known from the Ludlow and early Downton of

the Welsh Borderland. It seems likely, however, following the reasoning of Elliott (1978) and of Dineley and Loeffler, that cyathaspids occur earlier in Canada than in Europe. More work on the Canadian cyathaspids might help clarify their relationships and biostratigraphic significance.

DISCUSSION

Implications. As I predicted (Turner 1970), *T. macintoshi* is very closely related if not identical to the type thelodont *T. parvidens.* Also the type material contains *T. bicostatus* and *T. trilobatus.* These three scale forms, *T. parvidens, T. bicostatus* and *T. trilobatus,* are elements of the Baltic-Anglo-East Canadian Silurian fauna (the *T. parvidens* assemblage of Turner 1973). This assemblage may represent a facies fauna indicative of the onset of "red bed" conditions.

If the thelodonts do come from the Long Reach Formation and the age of the fish beds is confirmed as early Wenlock, or even late Llandovery, this will add weight to the predicted occurrence of *T. parvidens* throughout the southern Laurasian region in the early Silurian. The appearance of *T. parvidens* before the late Wenlock is disputed by Karatajute-Talimaa (1978), who has not found it in any of the older localities which she has investigated. However, the fact that *T. parvidens* did appear in the late Llandovery is confirmed by its discovery in the Norwegian succession. If this is the oldest occurrence then there must have been the possibility of dispersal of *T. parvidens* between the west Baltic, the Welsh Borderland and New Brunswick. This would imply a shallow water connection between at least two of these three regions in mid-Silurian times.

The *T. parvidens* assemblage could also represent a cline, with the *T. macintoshi* form to the "west" of the range in New Brunswick, and forms such as *T. costatus* (Pander 1856), *T. sculptilis* Gross 1967, and *T. admirabilis* Märss 1982 to the "east" in the southern Baltic—even, perhaps, including *T. marginatus* Karatajute-Talimaa 1978. *T. trilobatus, T. bicostatus,* and *T. pugniformis* Gross 1967 would be included in *T. parvidens* as varieties because all possess a similar histological structure. These thelodonts would be placed within Blieck's Ichthyofacies IIA (Blieck 1982). Blieck (1982, Fig. 5) envisaged the New Brunswick site as located within the Appalachian channel with a possible link to the Welsh Borderland and elsewhere

in western Europe via a narrow shallow water passage. New Brunswick was almost certainly in connection with the Anglo-Welsh cuvette, Norway and probably elsewhere in the Baltic hinterland at some point during late Llandovery to early Downton times (see also Turner and Tarling 1982).

Scales of *T. parvidens* have also been found in the Ludlow Moydart Formation of Nova Scotia (Ørvig in Boucot *et al.* 1974) and those of "*Thelodus* sp." in the Upper Silurian (Lower Devonian?) Oriskany Sandstone of Nictaux Falls, Nova Scotia (Eastman 1907, Gardiner 1966). Thus there are indications that the *T. parvidens* fauna was quite widespread in eastern Canada by late Silurian times.

Environment. Denison (1956); Robertson (1957); and White (1958) considered that the fauna at Nerepis indicated a marginal marine or non-marine environment. From the state of preservation it would seem that the animals were living in or near a quiet backwater, possibly a supratidal pool or a lagoon. The style of preservation in the New Brunswick fish beds is virtually identical to that in the Lower Silurian fish beds of southern Scotland (see e.g., Ritchie 1968). At Lesmahagow and Hagshaw thelodonts, anaspids, ceratiocarids, eurypterids and rare xiphosurans are found, often contained in nodules (considered to be coprolitic) within black shales. Some near-complete thelodonts are preserved in large nodules, and numerous scales occur in the center of nodules, probably the remains of consumed thelodonts. At Cunningham's Brook these coprolitic masses seem to be confined to one horizon (Denison's horizon B). There is little or no evidence of transport seen on any of the specimens; thelodont scales are not noticeably waterworn and a range of scale size is seen in the disarticulated scale masses in nodules as well as in articulated squamation (see Figs. 1, 2).

Denison (1964) discussed the state of preservation of the cyathaspids and found that one specimen, also found in a coprolite, was a juvenile on the evidence of its thin plates and scales. This also suggests that the fish were living and dying in a low-energy environment.

The large size of the thelodonts in the Nerepis fauna suggests that this was an ideal environment for these creatures which until now have invariably been thought of as small insignificant agnathans.

The thelodonts in the Lower Silurian of Scotland, belonging to *Loganella scotica* Traquair 1898, which seem to have lived in a similar environment, also exhibit a range of size from a few centimeters (juveniles) to quite large individuals (up to an estimated 400 mm). If similarity of faunal components and style of preservation are taken into account then the Nerepis site and Scottish lower fish beds could be of equivalent age, which would be late Llandovery to early Wenlock (e.g., Rolfe 1973).

ACKNOWLEDGMENTS

I would like to thank Mrs. Ruth Romer, Dr. and Mrs. R. H. Denison, Dr. W. E. Schevill and M. C. Schaff for their help and hospitality in Cambridge, Mass. Dr. Denison made helpful comments upon the manuscript. Dr. and Mrs. John Bolt, J. Clay Bruner, and Dr. and Mrs. W. Turnbull gave me their help and hospitality while I was in Chicago. The opportunity to examine the Field Museum material was provided by the award of a grant from the Thomas Dee Visiting Scientist Fellowship. Dr. Godfrey S. Nowlan helped me to obtain information on the geology of New Brunswick. Dr. Roger Miles allowed me to examine and cast the BMNH specimen then under his care. Part of this work was done under the auspices of an Honorary Research Fellowship of the Queensland Museum, for which I thank Dr. Alan Bartholomai and the Board of Trustees.

LITERATURE CITED

AGASSIZ, J. R. L. 1839. Fishes, p. 605. *In* R. I. MURCHISON. The Silurian System, founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester, and Stafford; with descriptions of the coal-fields and overlying formations. London: John Murray, xxxii + 768 pp.

BAILEY, L. W., AND W. MCINNES. 1888. Report on explorations and surveys in portions of northern New Brunswick and adjacent areas in Quebec, and in Maine. United States Annual Report, Geol. Natural Hist. Surv. Can. III, part II, Report M: 1–52.

BERRY, W. B. N., AND A. J. BOUCOT. 1970. Correlation of the North American Silurian rocks. Geol. Soc. Am. Spec. Pap. No. **102**: 1–289.

BLIECK, A. 1982. Les grandes lignes de la biogéographie des Hétérostracés du Silurien supérieur-Dévonien inférieur dans le domaine nord-atlantique. Palaeogeography, Palaeoclimatology, Palaeoecology, **38**: 283–316.

Boucot, A. J., J. F. Dewey, D. L. Dineley, R. Fletcher, W. K. Fyson, J. G. Griffin, C. F. Hickox, W. S. McKerrow, and A. M. Ziegler. 1974. The Geology of the Arisaig area, Antigonish County, Nova Scotia. Geol. Soc. Am. Spec. Pap. No. **139**: 1–191.

Denison, R. H. 1956. A review of the habitat of the earliest vertebrates. Fieldiana, Geology, **11**: 359–457.

———. 1964. The Cyathaspididae, a family of Silurian and Devonian jawless vertebrates. Fieldiana, Geology, **13**: 311–473.

Dineley, D. L., and E. J. Loeffler. 1976. Ostracoderm faunas of the Delorme and associated Siluro-Devonian formations, Northwest Territories, Canada. Spec. Pap. Palaeont. No. **18**: 1–218.

Eastman, C. R. 1907. Devonic fishes of the New York formations. Memoir of the N.Y. State Mus. Nat. Hist., Albany, **10**: 1–235.

Elliott, D. K. 1978. New Pteraspididae from the Canadian Arctic. p. 27. PADS Abstracts. International Symposium on the Devonian System 1978. The Palaeontological Assoc., Univ. Bristol: 61 pp.

Gardiner, B. G. 1966. Catalogue of Canadian fossil fishes. Roy. Ont. Mus. Life Sciences, Contrib. No. **68**: 1–154.

Goujet, D., and M. V. Locquin. 1979. Découverte de spores fongiques dans les écailles de poissons et d'agnathes paléozoïques: *Mycobystrovia lepidophaga* gen. et sp. nov. 104e Congrès National des Sociétés Savantes, Bordeaux, sciences, Fascicule **I**: 87–99.

Gross, W. 1967. Uber Thelodontier-Schuppen. Palaeontographica, **127A**: 1–64.

Halstead, L. B. and S. Turner. 1973. Silurian and Devonian ostracoderms, pp. 67–79. *In* A. Hallam (ed.), Atlas of Palaeobiogeography. Amsterdam: Elsevier, 531 pp.

Hoppe, K. H. 1931. Die Coelolepiden und Acanthodier des Obersilurs der Insel Oesel. Palaeontographica **76**: 35–94.

Karatajute-Talimaa, V. N. 1978. Silurian and Devonian Thelodonts of the USSR and Spitsbergen. Vilnius: Mosklas, 1–334 [in Russian].

Lawson, J. D. 1975. Ludlow Benthonic Assemblages. Palaeontology **18** (3): 509–525.

MacKenzie, G. S. 1951. Geol. Surv. Can. Pap. 1951–15 (out of print, not seen).

———. 1964. Geology, Saint John, New Brunswick. Geol. Surv. Can. Map 1113A, 1 inch: 1 mile, 1: 63360.

———. 1964. Geology, Hampstead, New Brunswick. Geol. Surv. Can. Map 1114A, 1 inch: 1 mile, 1: 63360.

Marss, T. 1982a. *Thelodus admirabilis* n. sp. (Agnatha) from the Upper Silurian of the East Baltic. Eesti NSV Teaduste Akadeemia Toimetised 31, K. Geol. no. **31**: 112–116.

———. 1982b. Vertebrate zones in the East Baltic Silurian, pp. 97–105. *In* D. Kaljo and E. Klaaman (eds.), Ecostratigraphy of the East Baltic Silurian. Tallinn: Academy of Sciences Estonian SSR, Inst. Geol.

Matthew, G. F. 1888. On some remarkable organisms of the Silurian and Devonian rocks in Southern New Brunswick. Proc. Trans. Roy. Soc. Can., Ottawa, Section 6 (1) **6**, Section 4: 49–62.

———. 1907. A new Genus and a New Species of Silurian Fish. Trans. Roy. Soc. Can. (3), **1**, section 4: 7–9.

McCutcheon, S. R. 1981. Revised stratigraphy of the Long Reach area, southern New Brunswick: evidence for major, northwestward-directed Acadian thrusting. Can. J. Earth Sciences, **18** (3): 646–656.

Pander, C. H. 1856. Monographie der fossilen Fische des silurischen Systems der russisch-baltischen Gouvernements. St. Petersburg: x + 1–91.

Powrie, J. 1870. On the earliest known vestiges of vertebrate life; being a description of the fish remains of the Old Red Sandstone of Forfarshire. Trans. Geol. Soc. Edinburgh, **1**: 284–301.

Ritchie, A. 1968. New evidence on *Jamoytius kerwoodi* White, an important ostracoderm from the Silurian of Lanarkshire, Scotland. Palaeontology, **11**, 1: 21–39.

Robertson, J. D. 1957. The habitat of early vertebrates. Biol. Rev. Camb. **32**: 156–87.

Rolfe, W. D. I. 1973. Excursions 14 and 15, Lesmahagow and Hagshaw Hills, pp. 105–126. *In* B. J. Bluck (ed.), Excursion Guide to the Geology of the Glasgow Districts. Glasgow Geol. Soc. Glasgow: 181 pp.

Smith, J. C. 1966. Geology of Southwestern New Brunswick. pp. 1–12. *In* W. H. Poole (ed.), Geology of parts of Atlantic provinces. Guidebook, Geol. Assoc. Can. Miner. Assoc., Halifax.

Stetson, H. C. 1928. A New American *Thelodus*. Amer. J. Science, **16**: 221–31.

Thorsteinsson, R. 1967. Preliminary note on Silurian and Devonian ostracoderms from Cornwallis and Somerset Islands, Canadian Arctic Archipelago, pp. 45–47. *In* Evolution des Vertébrés. Problems actuel de Paléontologie, 163, Paris: C. N. R. S. Masson et Cie.

Traquir, R. H. 1898. Report on Fossil Fishes. Summary of Progress for 1897, Geol. Surv. G. B., 72–76.

Turner, S. 1970a. Timing of the Appalachian/Caledonian orogen contraction. Nature, London, **227**, No. 5253: 90.

———. 1970b. Fish help to trace continental movements. Spectrum, Bull. Cent. Off. Inf., No. **79**: 8–10.

———. 1973. Siluro-Devonian thelodonts from the Welsh Borderland. J. Geol. Soc., **129**: 557–84.

———. 1976. Thelodonti (Agnatha), pp. 1–35. *In* F. Westphal (ed.), Fossilium Catalogus I: Animalia, Pars **122**: 114 pp.

———. 1982. A new articulated thelodont (Agnatha) from the Early Devonian of Britain. Palaeontology, **25** (4): 879–89.

———. 1984. Studies on Palaeozoic Thelodonti (Craniata: Agnatha). Unpublished Ph.D thesis, available from The Librarian, Univ. Newcastle-upon-Tyne.

———, and D. Tarling. 1982. Thelodont and other agnathan distributions as tests of Lower Palaeozoic continental reconstructions. Palaeogeography, Palaeoclimatology, Palaeoecology, **39**: 295–311.

Westoll, T. S. 1951. The vertebrate-bearing strata of Scotland, pp. 5–21. *In* The correlation of continental vertebrate-bearing rocks. Int. Geol. Cong. London, part 11, section K, report 18th sess., 93 pp.

WESTOLL, T. S. 1958. Stratigraphical Framework, pp. 235–239. *In* T. S. WESTOLL (ed.), Studies on Fossil Vertebrates. Univ. London: Athlone Press: 263 pp.

WHITE, E. I. 1958. Original Environment of the Craniates, pp. 212–234. *In* T. S. WESTOLL (ed.), Studies on Fossil Vertebrates. Univ. London: Athlone Press, 263 pp.

WHITLEY, G. P. 1976. More fish genera scrutinized. Aust. Zool. **19**: pp. 45–50.

WOODWARD, A. S. 1920. Presidential address. Proc. Linn. Soc. London, 132nd sess.: 25–34.

B R E V I O R A

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 29 AUGUST 1986 NUMBER 487

THE IDENTIFICATION OF LARVAL *PARASUDIS* (TELEOSTEI, CHLOROPHTHALMIDAE); WITH NOTES ON THE ANATOMY AND RELATIONSHIPS OF AULOPIFORM FISHES

KARSTEN E. HARTEL AND MELANIE L. J. STIASSNY[1]

ABSTRACT. Larvae and transforming individuals of *Parasudis* are identified and described for the first time. The phylogenetic integrity of the family Chlorophthalmidae is investigated and restricted to the sistergenera, *Parasudis* and *Chlorophthalmus*. Two derived morphological characters support the monophyly of an extended Ipnopidae which now includes the genus *Bathysauropsis*. The "rostral cartilages" in aulopiform fishes are reviewed and the homology of these and associated structures throughout the lower Neoteleostei is questioned.

INTRODUCTION

Parasudis truculenta (Goode and Bean, 1895) is a relatively common offshore fish found from off northern New England to equatorial Brazil. Adult specimens have been taken only in bottom trawls at depths of ca.180 to 480 m, but dietary studies suggest that *Parasudis* moves off the bottom to feed in midwater (Mead 1966). The species is hermaphroditic, and ripe specimens have been collected from February to May (Mead 1960). Neither the eggs nor the larvae of this species have yet been described (Okiyama 1984).

The purpose of this paper is to describe larval and transforming *Parasudis,* and to comment on aspects of anatomy and relationships. There is considerable confusion in current literature regarding

[1]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. Order of authorship is alphabetical.

the systematics and classification of Rosen's (1973) Aulopiformes (see Johnson 1982; Okiyama 1984; Rosen 1985; Stiassny 1986). The resolution of this problem is beyond the scope of this paper and for the purpose of this study we adhere to Rosen's classification of the Order (1973:509).

MATERIALS AND METHODS

Specimens are from the Woods Hole Oceanographic Institution (WHOI) collections housed at the Museum of Comparative Zoology, Harvard University (MCZ); the Atlantic Research Centre, New Brunswick (ARC); the DANA collections of the Zoological Museum, University of Copenhagen (ZMUC); the National Museum of Natural History, Washington, D.C. (USNM); the British Museum of Natural History (BMNH) and the University of Miami (UMML). The specimens used in this study are listed in appendix under material examined.

Counts and measurements follow Hubbs and Lagler (1964). For osteological examination, selected specimens were cleared and stained following the procedure of Dingerkus and Uhler (1977); these specimens are indicated "c.s." under material examined. Anatomical drawings were made with the aid of a Zeiss SV-8 stereomicroscope with a camera lucida attachment. Osteological and syndesmological nomenclature follows Stiassny (1986).

DIAGNOSIS

Parasudis larvae are characterized by the distinctive bulbous shape of the snout, the pattern of snout, opercular and caudal pigmentation, as well as by a particular basihyal form and dentition. The larvae are further distinguished from those of other chlorophthalmoid taxa by having 38 to 39 vertebrae and/or myomeres (Okiyama 1984:208).

DESCRIPTION

Larvae

(Figs. 1A, B and C)

Preflexion or flexion larvae are not present among the material examined, and the following description is based on 85 postflexion

specimens ranging from 10.6 to 80 mm standard length (SL). Specimens of 15.4 and 30.6 mm SL are illustrated in Figs. 1A–C. The body is elongate, oval to round in cross section at maximum depth; maximum depth 6.4 to 9.4 times in SL; maximum body width subequal or equal to maximum body depth (7.8 to 11.7 in SL). Head length (HL) 2.6 to 3.9 times in SL, probably negatively allometric. Bulbous snout rounded in anterodorsal profile, 2.2 to 3.0 times in HL. Eyes large, 3.5 to 5.0 times in HL. The eyes often appear stalked or partially stalked (Fig. 1B). The presence (or absence) of stalked eyes may be a result of damage incurred during collection; however, stalked and non-stalked specimens do appear in the same samples. The eyes of both larval and transforming individuals lack the "keyhole" shaped aphakic space characteristic of adult chlorophthalmids.

All larvae examined appear to have a full complement of fin elements, although, the fragile fin rays are often damaged. The origin of the dorsal fin (10 rays) is slightly posterior to the base of the pectoral fin (17 rays). The narrow-based adipose fin is positioned above the second or third anal ray (8–9 anal rays). The pectorals are at mid-body level with their bases almost under the thin opercular flap. Pelvic fin (9 rays) origin is below the anterior half of the dorsal fin. The caudal fin is forked even in the smallest specimens. Procurrent caudal rays are present and increase in number with growth. The anus is located well caudad of the pelvic fin base but closer to the insertion of the pelvic than to the insertion of the anal fin.

The dentition remains relatively constant throughout the larval period. Both the premaxillae and the dentaries bear single rows of evenly spaced caniniform teeth (Fig. 2). Anteriorly, these larval teeth are recurved, but are markedly retrose in the posterior aspect of both upper and lower jaws. Two to three small recurved caniniform teeth are implanted along the anteriolateral aspect of the dentary (Fig. 2).

In most specimens a few small caniniform teeth are inserted along the body of the palatine cartilages, and in the ventral hypobranchial apparatus a markedly elongate basihyal cartilage bears small recurved fang-like teeth on its anterior margin (Fig. 3A).

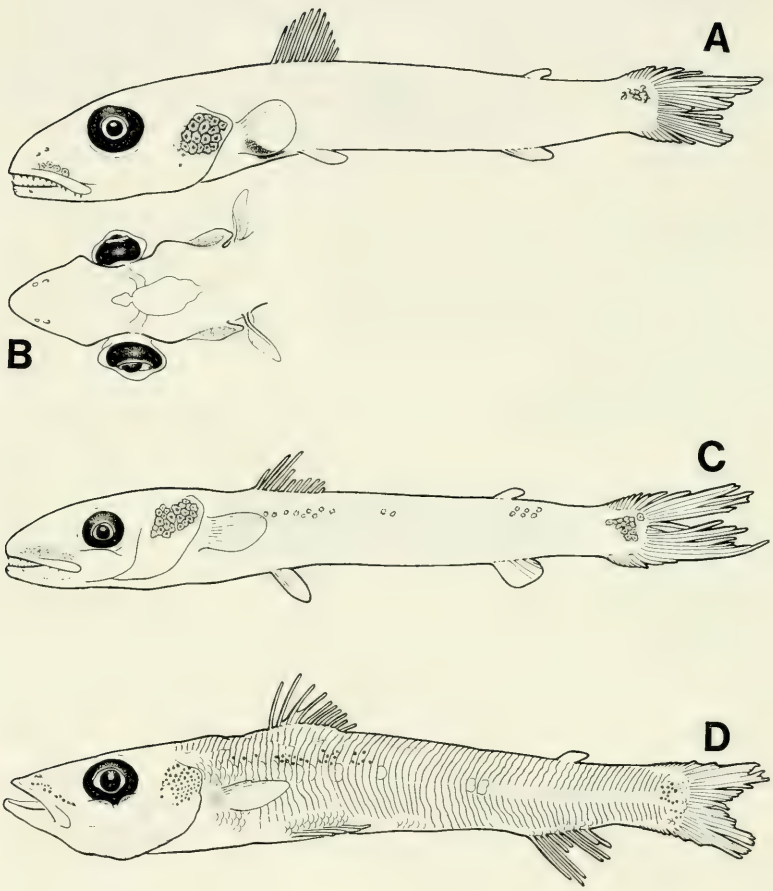


Figure 1. *Parasudis truculenta.* (A) Lateral view of larva 15.4 mm SL (MCZ 62400). (B) Dorsal view of head of same specimen. (C) Lateral view of larva 30.6 mm SL (MCZ 62399). (D) Lateral view of transforming juvenile 85 mm SL (MCZ 62401). Note that the dotted lines on the body in (A) and (C) represent myosepta while the solid lines in (D) represent the pigmented edges of scale pockets. Drawn by S. Landry.

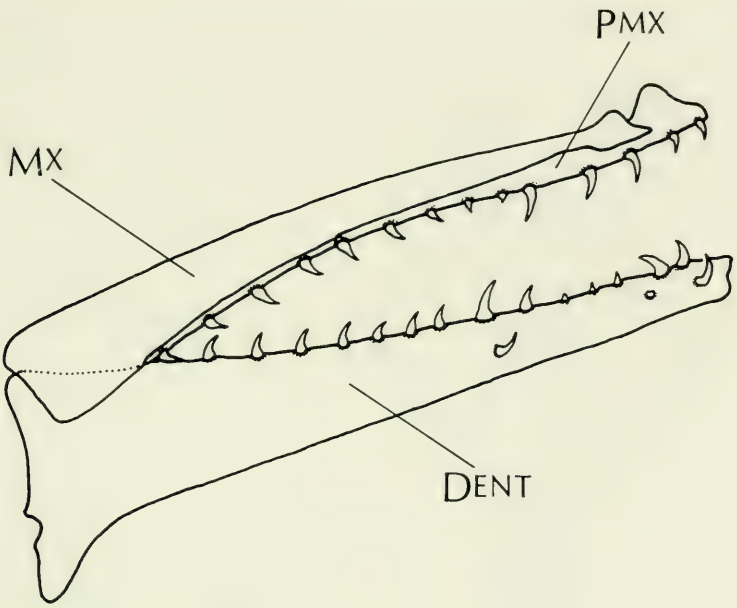


Figure 2. Isolated buccal jaws of larval *Parasudis* (MCZ 62397, 38 mm SL).

Abbreviations: Dent, dentary; Mx, maxilla; Pmx, premaxilla.

Pigmentation

Body color in preserved specimens is a uniform opaque white although very infrequently a light tan or brown wash is present. Live coloration is unknown, but based on observations of live pretransformation *Chlorophthalmus* (Hartel personal observation), living *Parasudis* larvae are presumed to be almost translucent in seawater.

Opercular pigmentation covers an area almost as large as that of the eye and at times may be quite dark. Opercular pigmentation is present in the smallest specimen examined.

Initially, a small group of melanophores is situated on the caudal peduncle above the midline. With growth (>30 mm SL) the pigmented area becomes roughly triangular in outline with the posterior lower corner extending below the midline (Fig. 1C). A melanophore distinct from the triangular patch and situated in the upper corner of the caudal base is found in specimens greater than 22 mm

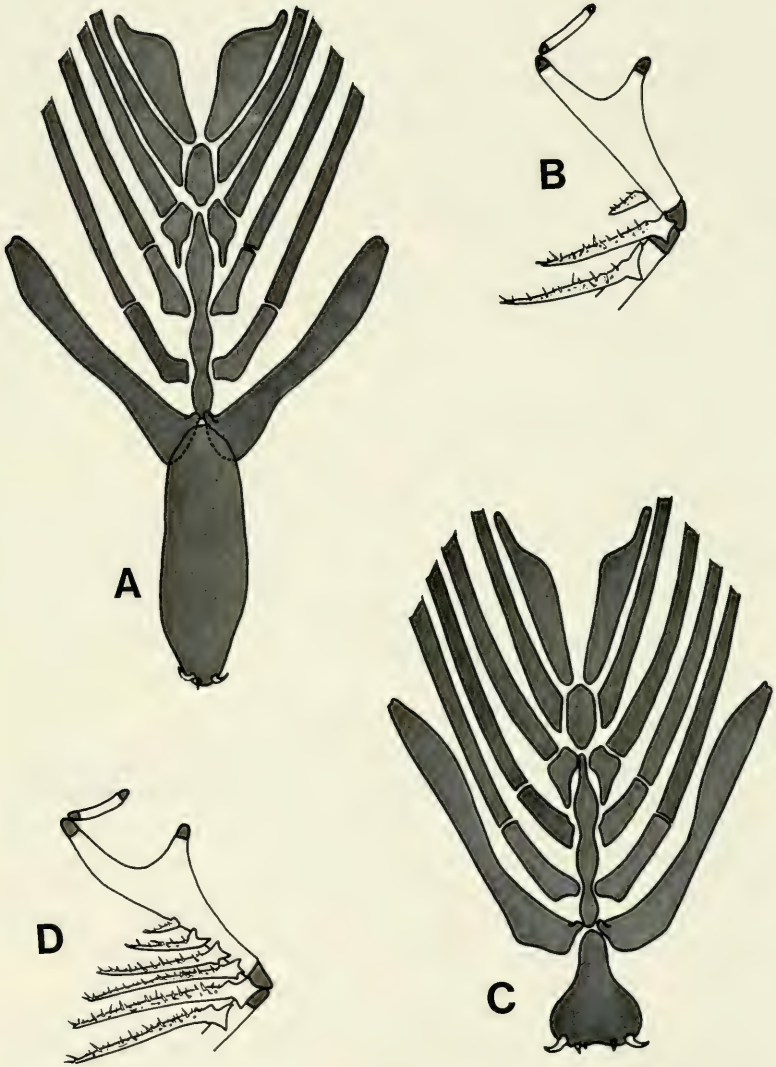


Figure 3. *Parasudis.* (A) Ventral gill arch elements and hyoid apparatus of larva 30 mm SL (MCZ 62398). (B) First epibranchial and associated structures of adult specimen (MCZ 40561). *Chlorophthalmus.* (C) Ventral gill arch elements of larva 22 mm SL (MCZ 62403). (D) First epibranchial and associated structures of adult specimen (MCZ 40509).

SL, and a second is usually developed at the lower corner of the caudal base by 30 mm SL.

Pigmentation in the snout region first appears as a single melanophore above the anterior end of the maxilla at 14 mm SL. Additional melanophores are added posteriorly in a line just above the maxilla and by 50 mm SL, the row reaches a point almost under the anterior margin of the orbit.

Lateral body pigmentation begins as one or two mid-body melanophores at 22 mm SL. The melanophores increase laterally in two groups. Four are present under the dorsal, and three are under the adipose fin by 24 mm SL. At 40 mm SL the melanophores, which are always found directly over a myomere, form an almost continuous band. There are one, two or sometimes three melanophores per myomere.

Deep pigment is present in the dorsal midline as a small dark spot just posterior to the dorsal fin. Ventrally a similar small midline spot is found at mid-body. An additional line of deep pigment is present along the midventral caudal peduncle. All of these deeper markings become less noticeable with growth as the muscle tissues become denser. Internal pigment is often visible through the bodywall below the base of the pectoral fin (Fig. 1A). This darkened area is densely pigmented mesentery supporting the viscera and areas of visceral peritoneum wrapping partially around the developing anterior viscera. The pigmented mesentary extends caudad almost to the level of the anal fin origin (Fig. 4).

Transforming specimens
(Fig. 1D)

This description is based upon two specimens, 75.5 mm SL (MCZ 57922) and 85 mm SL (MCZ 62401), illustrated in Fig. 1D. The larger specimen is only 5 mm larger than the largest available larval specimen (ARC 6879), yet marked morphological changes are evident.

General body proportions remain constant, but the form of the head is altered by the loss (via reabsorption?) of the characteristic bulbous larval snout. The smaller individual retains a few of the larval retrose jaw teeth and has a strong basihyal dentition. In the larger transforming fish the jaws are edentulate, apparently having lost the larval teeth and not yet having developed the juvenile/adult

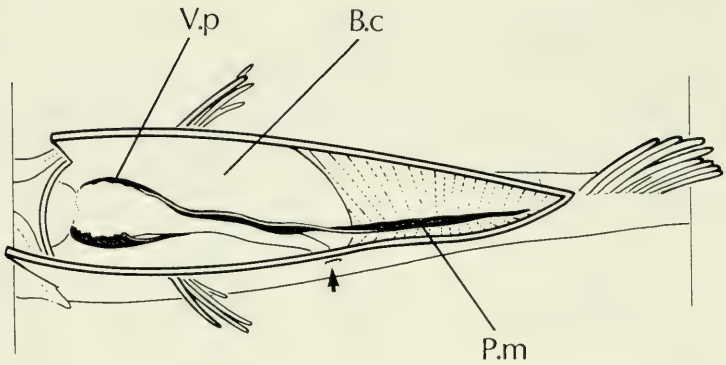


Figure 4. Internal pigmentation of larval *Parasudis* (based on two specimens; MCZ 63055, 40 mm SL and MCZ 63056, 31 mm SL). Drawn by S. Landry.

Abbreviations: B.c, body cavity; P.m, pigmented mesentery; V.p, visceral peritoneum.

dentition. A few small palatine teeth are present, and small teeth are embedded in the dermis overlying the basihyal element. As the smaller of the two transforming specimens is badly damaged and contorted, the remaining description is based solely upon the 85 mm SL specimen.

The diagnostic larval pigmentation pattern is faint but the remnants of snout, opercular, lateral and caudal pigmentation are still discernible. Patches of scales are present and, as is indicated in Fig. 1D, these have a distinctive pattern of implantation. Each scale pocket is located on a continuous flap of skin which is strongly pigmented along its distal margin. The resultant "herringbone" pattern is clearly visible in adult specimens (Mead 1966: Fig. 47) and where scales have been lost, corresponds to approximately two pigment lines per scale.

Transformation apparently occurs rapidly. We have seen a fully transformed juvenile (MCZ 41840) the same length as the larger transforming larva. The fully transformed fish has the definitive adult dentition (see Mead 1966), is scaled, and has lost almost all traces of larval pigmentation. During transformation the snout becomes increasingly flattened and "shrunken," lending the fish its characteristic "duckbilled" appearance. Apparently, a loss (reabsorption?) of the somewhat gelatinous larval body tissues results in a

more attenuated body form in the recently transformed juvenile. Halliday (1968: Fig. 1) illustrates a 99.0 mm SL transformed juvenile that shows initial body deepening.

The internal pigmentation of the anterior viscera is present in transforming specimens. Apparently during transformation, pigment migrates from the visceral peritoneum onto the parietal peritoneum, and the pigmentation of the caudad extension of the mesentery is greatly reduced. In fully transformed juveniles the parietal peritoneum is strongly pigmented throughout the abdominal cavity but little pigment is associated with the visceral peritoneum.

We have examined a number of transforming *Chlorophthalmus* specimens from both the North Atlantic Ocean and the Coral Sea. In each of these specimens, tranformation occurs at a considerably smaller size (ca. 35 to 40 mm SL) than that observed in our *Parasudis* specimens.

DISTRIBUTION

The western Atlantic specimens we have examined come from areas off the Brazilian coast to areas east of the southern tip of Nova Scotia (Fig. 5). Included in our study is one eastern Atlantic specimen (MCZ 62402). Preliminary morphometric analysis of this larva and its eastern Atlantic locality indicate that it may represent *Parasudis fraser-brunneri* (Poll 1953). However, due to a lack of additional material for detailed study and the close morphological resemblance of *P. fraser-brunneri* to *P. truculenta* (see Mead 1966:184), we are unable to confirm the specific identity of the eastern Atlantic specimen.

All of the larval *Parasudis* were taken in midwater trawls. Specimens from the WHOI opening and closing nets (MOC 10 and 20) indicate that the larvae are most commonly taken above 150 m (five collections: 70 to 0 m; 0 to 100 m; 70 to 140m; 0 to 203 m; 70 to 150 m). Information from non-closing nets indicate similar distributions. However, other collections taken with non-closing nets indicate that the larvae may approach the surface rather closely, since *Parasudis* larvae are found in collections taken above 50 m. Except for a few larvae from the relatively shallow Straits of Florida, all specimens were taken in trawls over ocean bottoms from 1937 to 4934 m deep.

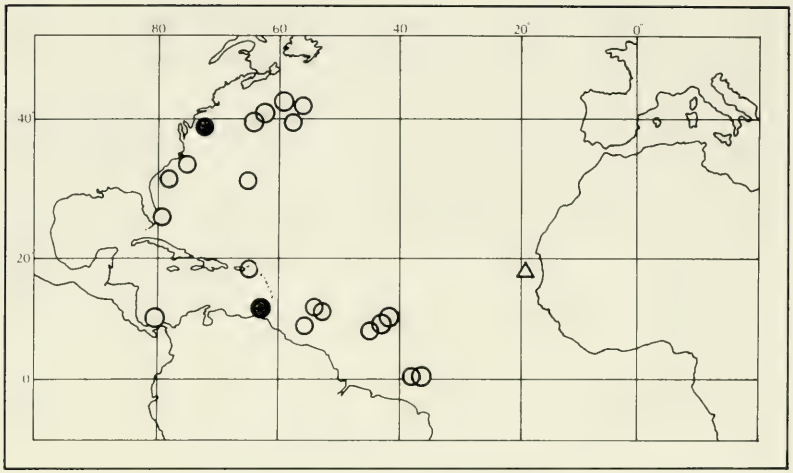


Figure 5. Distribution of larval *Parasudis* examined during this study. Open circles: *P.truculenta.* Solid circles: transforming larvae. Triangle: *P.?fraser-brunneri* larva (MCZ 62402). Symbols may represent more than one sample.

GENERIC PLACEMENT

As currently constituted the family Chlorophthalmidae (=Chlorophthalminae of Sulak 1977 and Nelson 1984) comprises three genera of benthic fishes (Okiyama 1984): *Chlorophthalmus* Bonaparte, 1840 (18+ species), *Parasudis* Regan, 1911 (two species) and *Bathysauropsis* Regan, 1911 (three species). Representatives of the former two genera inhabit the North Atlantic; *Bathysauropsis* is known only from the deep waters (2000 to 2500 m) of the South Atlantic and South Pacific (Mead 1966).

Based on adult morphology, Mead (1966) presented a key to chlorophthalmid genera; we note that *Parasudis* is further distinguished from the other two genera by having a single gill raker along the anterior border of the first epibranchial (Fig. 3B). In both *Chlorophthalmus* (Fig. 3D) and *Bathysauropsis,* the first epibranchial bears at least two or more lath-like denticulate gill rakers along its anterior margin.

Predorsal number distinguishes the three genera. Adult and larval *Parasudis* have a single predorsal bone (Figs. 6A, B). *Chlorophythalmus* have two (Figs. 6C, D), adult *Bathysauropsis* have three.

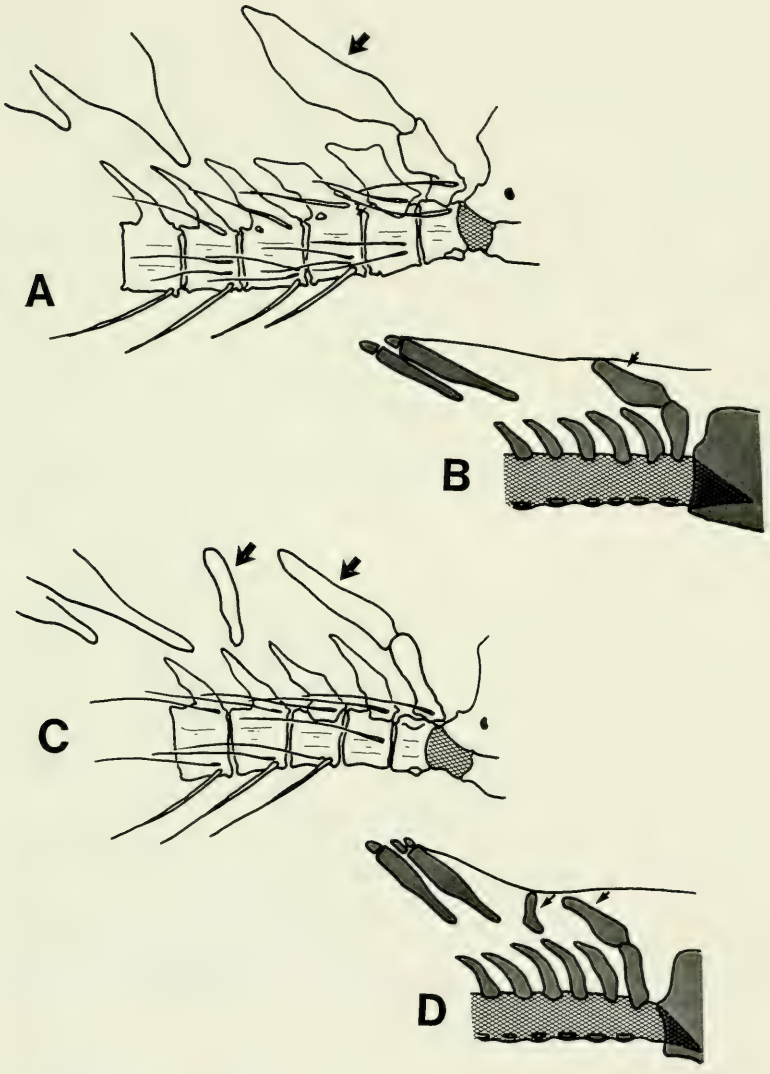


Figure 6. *Parasudis*. (A) Posterior region of the neurocranium, vertebral column and predorsal bones of adult specimen (MCZ 40561). (B) Larva 30 mm SL (MCZ 62398). *Chlorophthalmus*. (C) Posterior region of the neurocranium, vertebral column and predorsal bones of adult specimen (MCZ 41444). (D) Larva 22 mm SL (MCZ 62403). Arrows indicate predorsal bones.

Johnson (1982) discussed predorsal (=supraneural) number among aulopiforms and noted a trend towards predorsal reduction throughout the assemblage. He cited notosudids (=scopelosaurids) and *Omosudis* as other taxa with a single predorsal. Sulak (1977) stated that ipnopine genera bear one of two predorsals.

The anal position and lack of anal pigmentation during transformation of *Parasudis* contrasts with that of *Chlorophthalmus* where the anus is situated closer to the pelvic base (see Mead 1966), and is highly pigmented during transformation. Other pigment characters of the anterior visceral cavity separate *Parasudis* and *Chlorophthalmus*. In *Parasudis* the larval pigmentation is confined to the visceral peritoneum and associated mesentery, while in Chlorophthalmus it is a discrete patch closely associated with the parietal peritoneum which lines the body cavity. In addition, larval *Parasudis* differs from larval *Chlorophthalmus* by the presence in the former of a caudad extension of pigmented mesentry (Fig. 4). Deep visceral pigmentation in other aulopiforms is discussed by Johnson (1974).

COMPARISON WITH OTHER AULOPIFORM TAXA

To assess the phylogenetic significance of certain features described in *Parasudis* we compare them here with those found in *Chlorophthalmus* and other aulopiform taxa. Clearly, the following anatomical comparisons are far from exhaustive, and we have selected only those features which appear to be phylogenetically informative at the present level of analysis.

Rosen (1971) found basihyal teeth of a similar, although larger, form and distribution in larval *Chlorophthalmus* (see also our Fig. 3C), as well as in the ipnopid larvae he described (see Okiyama 1981 for other ipnopid larvae). Sulak (1977) described comparable basihyal dentition in larval *Bathypterois,* and *Bathytyphlops*. Rosen (1971) noted that a similar basihyal dentition is unknown in any adult fish (although the pattern is approximated in *Glossanodon*). Sulak (1977:80) stated that the "...condition appears to be unique to the juvenile stages of basal myctophiform fishes." However, until the full limit of the distribution of this type of larval dentition are known, particularly in larval aulopids and neoscopelids, we can draw little phylogenetic inference from its occurrence in *Parasudis* larvae.

Basihyal morphology easily distinguishes *Chlorophthalmus* from *Parasudis,* which in *Chlorophthalmus* is short and strongly spatulate (Figs. 3A, C), and in *Parasudis* is elongate. These differences, although less markedly than in larvae, are present in the ossified adult elements and help to distinguish the taxa (compare Figs. 7B, C). Basihyal morphologies similar to those of larval *Chlorophthalmus* are found in the larvae of *Bathypterois* (Sulak 1977; personal observation) and other ipnopids (Rosen 1971; Okiyama 1981), as well as in adult *Aulopus, Bathysaurus* and *Scopelosaurus* (Bertelsen *et al.,* 1976; personal observation). Thus, based upon its limited distribution, we interpret the broad and elongate basihyal of larval *Parasudis* as an autapomorphic feature.

Interestingly, adult ipnopids share a derived condition of the basihyal element, which is relatively tiny [or entirely absent in some bathypteroids (Mead 1966)] and obliquely aligned (Fig. 7A). A similar condition of the basihyal is present in adult *Bathysauropsis,* where unfortunately the larval condition is unknown (Okiyama 1984).[2]

Certain stomiatoids have a similar basihyal arrangement, however, we agree with Weitzman (1974) that the presence of a moderately sized and horizontally aligned basihyal is primitive for the Stomiiformes as a whole. Among alepisauroids (*sensu* Rosen 1973), a small (toothed) basihyal is found in certain scopelarchid taxa (Johnson 1974) and in *Bathysaurus,* but a small vertically aligned basihyal appears to be restricted in its distribution among aulopiforms to adult *Bathysauropsis* and the Ipnopidae.[3] The common occurrence of this basihyal morphology suggests an immediate common ancestry between them.

Corroboration of the phyletic integrity of a grouping comprising *Bathysauropsis* and the ipnopids is found in the degree of development of the branchiostegal membranes and gular fold. Mead (1966:115) described the region in bathypteroids in the following

[2]We have been able to examine only two specimens of *Bathysauropsis gracilis* but have kindly been given access to notes and radiographs made by K. Sulak after his examination of specimens of *B. gigas* and *B. mayanus.*

[3]Following Johnson (1982) and Okiyama (1984) the Ipnopidae is taken here to include the Bathypteroidae of Mead (1966) and is equivalent to the Bathypteroidae of Marshall and Staiger (1975) and the sub-family Ipnopinae of Sulak (1977) and Nelson (1984).

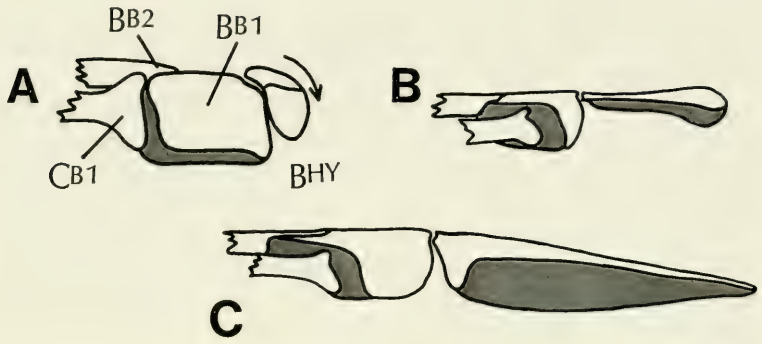


Figure 7. Basihyal and associated structures in adult (A) *Bathypterois* (MCZ 57624). (B) *Chlorophthalmus* (MCZ 41444). (C) *Parasudis* (MCZ 40561).

Abbreviations: Bb1–2, basibranchials 1–2; Bhy, basihyal; Cb1, ceratobranchial 1.

terms which apply equally to *Bathysauropsis* and the ipnopids: "Branchiostegal membranes broad and separate from one another and from the isthmus, overlapping anteriorly, and crossed near the tip of the jaw by a thick but narrow gular fold. . . " This morphology appears to be unique among aulopiforms and although a poorly developed gular fold is present in some stomiiform fishes (e.g., *Gonostoma* and *Polymetme*) it is not as elaborate as that found in *Bathysauropsis* and the ipnopids.

Chlorophthalmus shares with *Parasudis* the pigmented scale pocket skin flap character. In *Parasudis* the dorsal and ventral scale rows converge rostrad, "herringbone" fashion, upon the lateral line (Mead 1966; Fig. 47), while in *Chlorophthalmus,* dorsal and ventral scale rows diverge from the midline resulting in a slightly "zig-zag" pattern (Mead 1966; Fig. 46). This highly distinctive feature of squamation is unique to *Parasudis* and *Chlorophthalmus,* and is here interpreted as a synapomorphy uniting the two genera.

In the eyes of adult *Chlorophthalmus* (Theisen 1965; Fig. 3), as well as in adult *Parasudis,* a "keyhole" shaped aphakic space is present. Although well-developed aphakic spaces are not uncommon to the eyes of many benthic marine fishes (Munk 1966; Marshall 1971), a "keyhole" shaped space is restricted to adults of these

two genera. A similar space is absent in the eyes of *Bathysauropsis* and it is here interpreted as a synapomorphy of *Parasudis* and *Chlorophthalmus*.

RELATIONSHIPS

In reviewing the literature pertaining to *Parasudis* and its supposed relatives, it is clear that many problems remain (Johnson 1982; Rosen 1985; Stiassny 1986). However, at the intrafamilial level, aside from the suggestion that *Parasudis* may share a close phylogenetic relationship with paralepidid alepisauroids (Mead 1966), most authors who have considered the chlorophthalmids (e.g., Gosline *et al.* 1966; Marshall and Staiger 1975; Sulak 1977; Nelson 1984; Stiassny 1986) imply that *Chlorophthalmus* and *Parasudis* are closely related, and our own investigation confirms a sister-group relationship between these two taxa. The genus *Bathysauropsis* is poorly known anatomically, and consequently, its phylogenetic placement is less clear. Mead (1966) suggested that further investigation of this genus may indicate a need for familial reallocation, a finding that is corroborated by this study. We propose that the notion of an "intermediate" or "transitional" position of *Bathysauropsis,* forming a "link" between *Parasudis* and *Chlorophthalmus* on the one hand and the ipnopids on the other, and thus serving as "...the primary basis of the present incorporation of the ipnopine genera into the Chlorophthalmidae" (Sulak 1977:64) be replaced by a phylogenetic scheme in which *Bathysauropsis* is removed from the Chlorophthalmidae and incorporated within the Ipnopidae (Fig. 8). This relocation of *Bathysauropsis* is based on our observations of the presence of a small, obliquely aligned basihyal and a well-developed gular fold (Fig. 8: characters one and two). The position of *Aulopus* in relation to these taxa is here unresolved; larval aulopid material was unavailable for this study. Elsewhere Stiassny (1986) argued that *Chlorophthalmus, Parasudis* and *Aulopus* (but not *Bathysauropsis* and the other ipnopid genera) share with ctenosquamate fishes an advanced type of palatine/maxillary association and morphology (see also Rosen 1985 for a consideration of aulopid relationships). For this reason *Aulopus* is included in our cladogram, albeit in an unresolved position (Fig. 8).

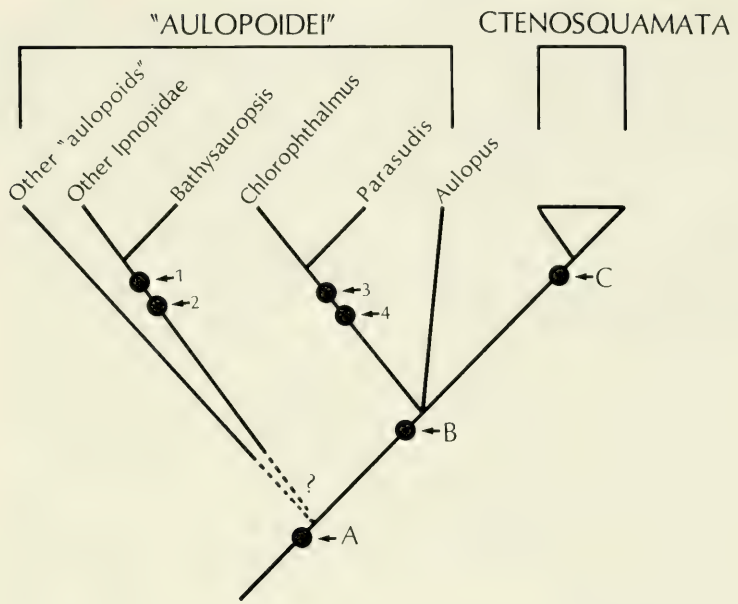


Figure 8. Cladogram of eurpterygian relationships, incorporating the results of the present study. Characters are the presence of: 1) A small obliquely aligned basihyal bone; 2) A thick well-developed gular fold; 3) A "keyhole" shaped aphakic space; 4) A peculiar scale pocket morphology and pigmentation; A) See Rosen (1985) for synapomorphies uniting the Aulopoidei with the Ctenosquamata; B) See Stiassny (1986) for synapomorphies uniting *Aulopus, Chlorophthalmus* and *Parasudis* with the Ctenosquamata; C) See Lauder and Liem (1983) for synapomorphies uniting the Ctenosquamata. Note: Following Rosen (1973), "other aulopoids" are the Bathysauridae and Notosudidae. "Other Ipnopidae" are *Bathypterois, Bathytyphlops, Bathymicrops* and *Ipnops*.

Significance of the Rostral Cartilage

Given this admittedly tentative scheme of relationships for the chlorophthalmids, it is extremely interesting to note the highly varied condition of the so-called "rostral cartilage" in these and in other aulopiform taxa. The "rostral cartilage" of both larval and adult *Parasudis* is a single median structure which is bound by a well-developed ethmo-rostroid ligament to both the ethmoid and premaxillae (Figs. 9A, B). The attachment of the cartilage to the ethmoid is strong in the larval fish and becomes weaker with growth. In

Parasudis, the rostral cartilage stains normally with Alcian Blue and is therefore presumably fully chondrified hyaline cartilage. In contrast, the "cartilage" in *Chlorophthalmus* (Figs. 9C, D; Rosen 1985; Fig. 40C) is paired, and the "cartilages" are associated with the symphyseal processes of the premaxillae. An ethmo-rostroid ligament is lacking, but the whole region is invested with loose connective tissue fibers. These rostral structures do not stain normally with Alcian Blue; staining is weak and diffuse. Similarly, in *Aulopus* (Rosen 1985; Fig. 41C; Stiassny 1986; Fig. 6) the single median structure does not stain as hyaline cartilage and is highly fibrous. Theisen (1965) illustrated paired rostral structures in *Ipnops* similar to those of *Chlorophthalmus.* Rosen (1985) also illustrated paired "rostral cartilages" of an apparently remarkably similar type and arrangement in the stomiiform, *Maurolicus.* Other stomiiform taxa examined in this study either lack a "rostral cartilage" entirely (e.g., *Photichthys*), or bear a single median structure ligamentously bound to the ethmoid region (e.g., *Gonostoma* and *Diplophos*). We have been unable to locate "rostral cartilages" in either *Bathypterois* or *Bathysauropsis.* In both of these genera the premaxillae are bound to the ethmoid region by a well-developed ethmo-rostroid ligament. We interpret the similarities between the rostral morphologies of *Chlorophthalmus* and *Ipnops* (and *Maurolicus*) to be homoplasious. To assess them otherwise, that is, to argue for the phyletic alignment of *Chlorophthalmus* with *Ipnops* (and *Maurolicus*) on the basis of this one "rostral cartilage" character would require losses and reversals in a series of other characters (see Fink and Weitzman 1982; Marshall and Staiger 1975).

Bertelsen *et al.* (1976) described and illustrated the rostral morphology of certain notosudids where a large (often ossified) "rostral cartilage" is bound to the ethmoid and the premaxillae by a well-developed ethmo-rostroid ligament similar to that of the stomiiform, *Gonostoma* (Stiassny 1986), or to that illustrated here for *Parasudis.*

Rostral morphologies are also confusing among other aulopiform lineages; for example, among synodontids, *Synodus* (Fig. 10A) bears a large medial and fully chondrified "rostral cartilage" strongly bound to the ethmoid. *Saurida* (Fig. 10B), on the other hand, lacks the structure as do both *Harpadon* and *Bathysaurus.* The paralepidid *Sudis* bears small paired hyaline cartilages, which in adults are associated with the symphyseal processes of the pre-

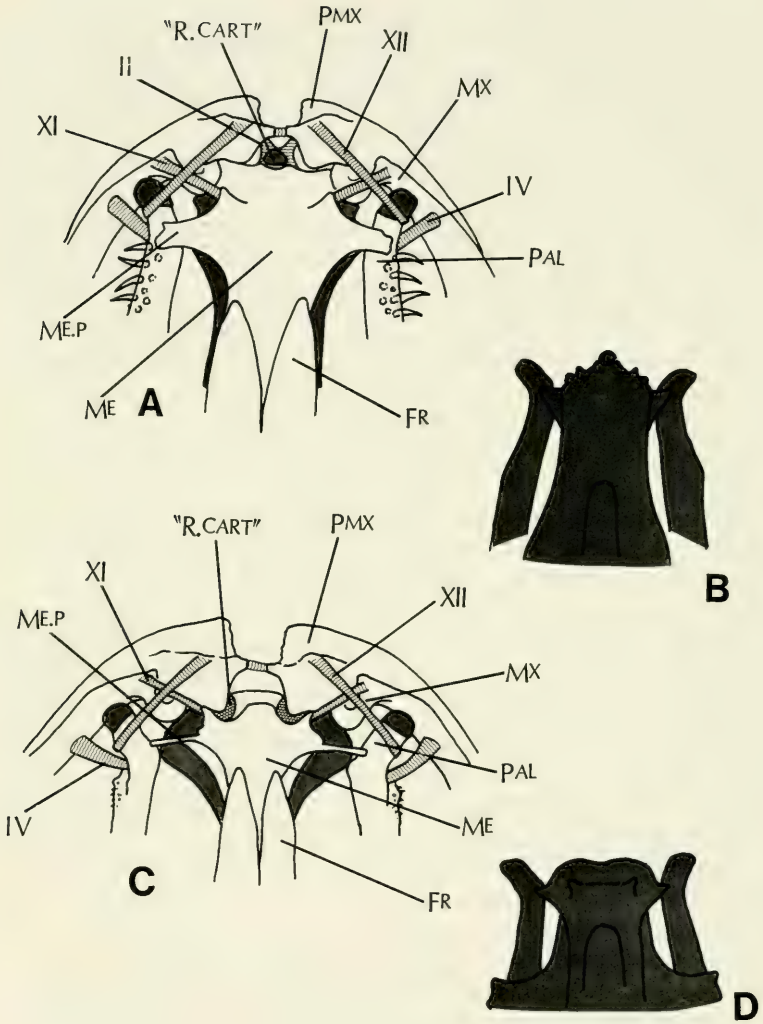


Figure 9. *Parasudis.* (A) Ethmovomer and upper jaws of adult specimen in dorsal view (MCZ 40561). (B) Ethmovomer of larva 30 mm SL (MCZ 62398) in dorsal view. *Chlorophthalmus.* (C) Ethmovomer and upper jaws of adult specimen (MCZ 40564) in dorsal view. (D) Ethmovomer of larva 22 mm SL (MCZ 62403) in dorsal view.

maxillae. In larvae these structures appear more strongly bound to the ethmoid. Finally, in *Alepisaurus* a condition much like that described in *Salmo* (Fink and Weitzman 1982; Rosen 1985) pertains. Paired hyaline cartilages are strongly bound to the inner faces of the premaxillary symphyseal processes.

Even from this cursory review it is clear the homologies of rostral morphologies and other associated structures throughout the lower Neoteleostei are questionable. By the level of the Acanthomorpha, the situation has stabilized such that there appears little doubt of the homology of the single median chondrified rostral cartilage strongly bound to the premaxillary ascending processes by a well-developed maxillo-rostroid ligament (Stiassny 1986). Until the distribution and homologies of the non-acanthomorph rostral structures are better understood, perhaps the term rostral cartilage should be restricted to that structure in the Acanthomorpha. When referring to the various rostral structures in non-acanthomorph neoteleosts before their homologies are resolved, the term "rostral cartilage" or "rostral structure" should be employed within quotation marks.

ACKNOWLEDGMENTS

We would like to thank the following individuals and institutions for the loan of material and/or helpful information and comments:

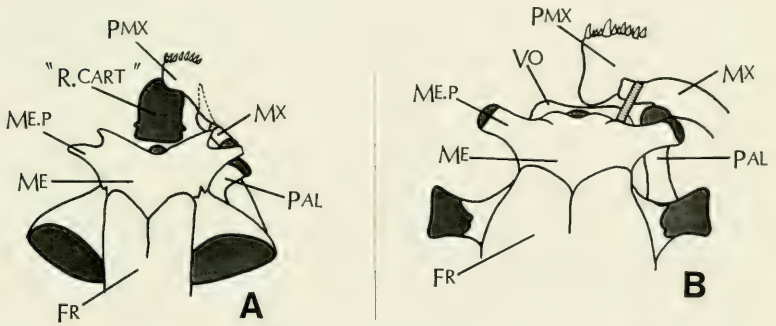


Figure 10. Ethmovomer and upper jaw of adult specimens of (A) *Synodus* (MCZ 47490). (B) *Saurida* (MCZ 56111).

Abbreviations: Fr, frontal; Me, mesethmoid; Me.p, mesethmoid process; Mx, maxilla; Pal, palatine; Pmx, premaxilla; "R.cart", "rostral cartilage". Ligaments: II, ethmo-rostroid; IV, median palato-maxillary; XI, ethmo-maxillary; XII, palato-premaxillary.

E. Bertelsen (ZMUC), R. H. Gibbs and R. P. Vari (USNM), R. K. Johnson (FMNH), D. F. Markle (formerly ARC), K. J. Sulak (ARC), J. Webb (Boston University), and A. Wheeler (BMNH). For their critical review of the manuscript we are grateful to J. E. Craddock (WHOI), G. D. Johnson (USNM), and K. F. Liem (MCZ). The late Sally Richardson offered invaluable comments on this paper and we dedicate our first work on larval fishes in her memory. We are especially grateful to Sally Landry for her skillful preparation of Figures 1 and 4.

This research was carried out during the tenure of NSF BSR 84-07449 (MLJS). NSF DEB 77-23726 (K. F. Liem) provided support for the transfer, sorting and curation of the WHOI specimens used in the study.

LITERATURE CITED

Bertelsen, E., G. Krefft and N. B. Marshall. 1976. The fishes of the family Notosudidae. Dana Rept., **86:** 3–114.

Dingerkus, G. and L. D. Uhler. 1977. Enzyme clearing of Alcian Blue stained whole small vertebrates for demonstration of cartilage. Stain Tech., **52**(4): 229–232.

Fink, W. L. and S. H. Weitzman. 1982. Relationships of the stomiiform fishes (Teleostei), with a description of *Diplophos*. Bull. Mus. Comp. Zool., **150**(2): 31–93.

Gosline, W. A., N. B. Marshall and G. W. Mead. 1966. Order Iniomi. *In* Fishes of the Western North Atlantic. Mem. Sears Fdn. mar. Res., **1:** 1–18.

Halliday, R. G. 1968. Occurences of *Parasudis trunculentus* (Goode and Bean) 1895 (Iniomi: Chlorophthalmidae) off La Have Bank, Nova Scotia. J. Fish. Res. Bd. Canada, **25**(2): 421–422.

Hubbs, C. L. and K. F. Lagler. 1964. Fishes of the Great Lakes Region. Ann Arbor: Univ. Michigan Press, 213 pp.

Johnson, R. K. 1974. A revision of the alepisauroid family Scopelarchidae (Pisces: Myctophiformes). Fieldiana (Zool.) **66:** 1–249.

———. 1982. A revision of the alepisauroid families Evermannellidae and Scopelarchidae: Systematics, morphology, interrelationships and zoogeography. Fieldiana (Zool.) N. S. **12:** 1–252.

Lauder, G. V. and K. F. Liem. 1983. The evolution and relationships of the actinopterygian fishes. Bull. Mus. Comp. Zool., **150:** 95–197.

Marshall, N. B. 1971. Explorations in the lives of fishes. Cambridge: Harvard Univ. Press, 204 pp.

Marshall, N. B. and J. C. Staiger. 1975. Aspects of the structure, relationships and biology of the deep-sea fish *Ipnops murrayi* (Family Bathypteroidae). Bull. Mar. Sci., **25**(1): 101–111.

MEAD, G. W. 1960. Hermaphroditism in archibenthic and pelagic fishes of the order Iniomi. Deep-Sea Research, **6:** 234–235.

———. 1966. Family Chlorophthalmidae. *In* Fishes of the Western North Atlantic, Mem. Sears Fdn. mar. Res., **1:** 162–189.

MUNK, O. 1966. Ocular anatomy of some deep-sea teleosts. Dana Rept., **70:**1–62.

NELSON, J. S. 1984. Fishes of the World. 2nd Ed. New York: Wiley and Sons, ix + 523 pp.

OKIYAMA, M. 1981. A larval Ipnops and its possible metamorphosis. Jap. J. Ichthyol., **28**(3): 247–253.

———. 1984. Myctophiformes:Development. *In* H. G. Moser, (ed.-in-chief), Ontogeny and Systematics of Fishes. Spec. Publs. Am. Soc. Ichthyol. Herptol., **No.1:** 206–218.

ROSEN, D. E. 1971. The Nacristiidae, a Ctenothrissiform family based on juvenile and larval scopelomorph fishes. Am. Mus. Novit., **2452:** 1–22.

———. 1973. Interrelationships of higher euteleostean fishes. *In* Greenwood, P. H., R. S. Miles, and C. Patterson (eds.), Interrelationships of Fishes. Zool. J. Linn. Soc. 53 Suppl. **1:** 397–513.

———. 1985. An essay on euteleostean classification. Am. Mus. Novit., **22877:** 1–45.

STIASSNY, M. L. J. 1986. The limits and relationships of the acanthomorph teleosts. J. Zool., Lond., (B)**1:** 1–50.

SULAK, K. J. 1977. The systematics and biology of *Bathypterois* (Pisces, Chlorophthalmidae) with a revised classification of benthic myctophiform fishes. Galathea Rept., **14:** 49–108.

THEISEN, B. 1965. On the cranial morphology of *Ipnops murrayi* Gunther, 1878 with special reference to the relations between the eyes and the skull. Galathea Rept., **8:** 7–17.

WEITZMAN, S. H. 1974. Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatoid families. Bull. Am. Mus. Nat. Hist., **153**(3): 329–478.

APPENDIX

MATERIAL EXAMINED

Parasudis material

The single figure given in parenthesis after the catalogue number is SL; if more than one specimen is registered the number of specimens is given and followed by their size range.

P. truculenta

Larvae: ARC uncat. (42.8 mm), 42°27′N 58°27′W, 0–300 m, 4 Apr. 1979, USSR Belogorsk, sta. 35–4. ARC 6729 (37.3 mm), 40° 22′N 62°38′W, 0–200 m, 20 Mar. 1979. ARC 6732 (28.0 mm, c.s.), 40°

51′N 61°34′W, 0–50 m, 21 Mar. 1979. ARC 6845 (41.2 mm), 39°44′N 56°59′W, 0–200 m, 1 Apr. 1979. ARC 6879 (80.0 mm), 42°27′N 58° 27′W, 0–300 m, 4 Apr. 1979. MCZ 58531 (28.5 mm), JEC 7755, 11° 12′N 53°49′W, 60 m, 27 Mar. 1977. MCZ 62397 (38.0 mm, c.s.), JEC 7715, 0°13′N 35°44′W, 90–100 m, 15 Mar. 1977. MCZ 62398 (30.0 mm, c.s.), JEC 7750, 10°48′N 52°17′W, c.80 m, 26 Mar. 1977. MCZ 62399 (30.6 mm), JEC 7753, 10°48′N 52°17′W, c.140 m, 27 Mar. 1977. MCZ 62400 (15.4 mm), MOC 10–118, 3, 34°12′N 75°00′W, 70–0 m, 14 Aug. 1978. MCZ 63055 (40.0 mm), JEC 7737, 38°55′N 72° 25′W, 0–825 m, 3–4 Sept. 1976. MCZ 63056 (31.0 mm), JEC 7738, 38°51′N 72°27′W, 0–750m, 4 Sept. 1976. Plus an additional 32 uncatalogued MCZ specimens (11.7–49.1 mm) from the WHOI collection. USNM 258610 (20.0 mm), 31°50′N 63°56′W, 40 m, 23 Feb. 1972.

(ZMUC) DANA 1166V (11, 14.6–24.1 mm), 100 meters of wire out (mw) and DANA 1166VI (2, 14.3–21.2 mm), 50 mw, both 10° 16′N 40°41′W, 11 Nov. 1921. DANA 1168IV (41.4 mm), 300 mw, and DANA 1168VI (22, 13.8–23.9), 50 mw, both 9°30′N 42°41′W, 12 Nov. 1921. DANA 1190VIII (13.1 mm), 17°58′N 64°45′W, 100 mw, 13 Dec. 1921. DANA 11941 (10.6 mm), 17°58′N 64°41′W, 320 mw, 12 Dec. 1921. DANA 1202IV (12.5 mm), 100 mw, and DANA 1202 (11.3 mm), 50 mw, both 9°40′N 79°56′W, 10 Jan. 1922.

Transforming larvae: MCZ 57922 (75.5 mm), 11°36′N 62°46′W, 530m, 19 Apr. 1960. MCZ 62401 (85.0 mm) MOC 20–19, 0, 39°13.5′N 71°17.6′W, 0–1027m, 15 June 1982.

Adults: MCZ 39968 (9, 130–190 mm), 07°10′N 53°07′W, 360 m, 6 Nov. 1957. MCZ 40561 (22, 90–175 mm), 07°34′N 54°50′W, 360 m, 6 Nov. 1957. MCZ 40561 (3, 90–102.2 mm c.s.), 07°34′N 54°50′W, 6 Nov. 1957. MCZ 41840 (85.0 mm), 18°16′N 67°17′W, 450 m, 6 Oct. 1959. UMML 15608 (120 mm, c.s.) no data.

P. fraser-brunneri

Larvae: MCZ 62402 (31.5 mm), RHB 2053, 16°32′N 19°35′W, 50–56 m, 13 Nov. 1970.

Adults: USNM 245646 (3, 84–138), 04°26′N 08°29′W, 200 m., 31 Oct., 1963, BBC 843. MCZ 63153 (3, 97–105, one specimen c.s.), same data as USNM 245646.

Comparative material

STOMIIFORMES

Gonostomatidae—*Diplophos taenia:* MCZ 52562, MCZ uncat. c.s.; *Gonostoma elongatum:* MCZ 62404; *Gonostoma sp.:* MCZ uncat. c.s.

Sternoptychidae—*Maurolicus muelleri:* MCZ 62598, MCZ uncat. c.s.

Photichthyidae—*Photichthys argenteus:* MCZ 56953; *Polymetme corytheola:* MCZ 56968, MCZ uncat. c.s.

AULOPIFORMES

Aulopidae—*Aulopus nanae:* MCZ 40516; *A. japonicus:* MCZ 45169 c.s.

Chlorophthalmidae—*Chlorophthalmus agazzisi:* MCZ 40539, MCZ 40509 c.s., MCZ 41444 c.s.;*C. bicornis:* BMNH 1939.5.24:457; *C. brasiliensis:* MCZ 51365, MCZ 40564 c.s.; *C. chalybeius:* MCZ 62155, MCZ 40564 c.s.; *C. nigripinnis:* BMNH 1887.12.7:207; *Chlorophthalmus* sp.: MCZ 62403 c.s., MCZ 62591, MCZ 62592, MCZ 62593, MCZ 62597.

Ipnopidae—*Ipnops murrayi:* MCZ 41133; *Bathypterois phenax:* MCZ 57624; *B. quadrifilis:* MCZ 35598; *B. viridensis:* MCZ 40567 c.s.; *Bathysauropsis gracilis:* BMNH 1887.12.7:209–210.

Notosudidae—*Scopelosaurus argenteus:* MCZ 62405 c.s., MCZ 62406 c.s.; *S. harryi:* MCZ 40512.

Scopelarchidae—*Scopelarchus analis:* MCZ 62599 c.s.

Bathysauridae—*Bathysaurus agazzisi:* MCZ 55305 c.s., MCZ 62409 c.s.; *B. mollis:* MCZ 41140

Synodontidae—*Synodus synodus:* MCZ 47378, MCZ 47490 c.s.; *S. jaculum:* MCZ 46972 c.s.; *Saurida brasiliensis:* MCZ 62408 c.s.; *Sa. tumbil:* MCZ 59273; *Sa. undosquamis:* MCZ 56111 c.s.

Harpadontidae—*Harpadon* sp.: MCZ uncat. c.s.

Alepisauridae—*Alepisaurus brevirostris:* MCZ 60345, MCZ 43153 c.s.

Evermanellidae—*Evermanella* sp.: MCZ uncat. c.s.

Paralepididae—*Paralepis elongata:* MCZ 43140; *P. speciosa:* MCZ 60332 c.s.; *Lestrolepis intermedia:* MCZ 62407 c.s.; *Sudis atrox:* MCZ 60336 c.s.

Harvard MCZ Library
3 2044 066 302 829

Date Due

NOV 30 1987